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ALL FORMS OF LIFE IN RELATION TO ENVIRONMENT

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TABLE OF CONTENTS, VOLUME XIV, 1933

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ERRATA

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P. 263. Shaw article. Throughout, change *Girardinus guppyi* to *Lebistes reticulatus* and *Platypoecilus rubra* to *Platypoecilus maculatus*.

P. 336, Fig. 1. Transfer this graph to fig. 6. This is the graph of the rhythmic activity of *Boletotherus cornutus* in total darkness.

P. 341, Fig. 6. Transfer this graph to fig. 1. This is the graph of the nocturnal activity of *Parcoblatta pennsylvanica* under relatively normal conditions.

VOLUME XIV, No. 3, 1933

P. 248, Fig. 1. Transfer this cut to Fig. 2.
P. 249, Fig. 2. Transfer this cut to Fig. 1.
P. 402, Table I. For *Pelleae* read *Pellaea*.

ECOLOGY

VOL. XIV JANUARY, 1933 No. 1

FOREST ASSOCIATIONS IN THE UPLANDS OF THE LOWER GULF COASTAL PLAIN (LONGLEAF PINE BELT)

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Interesting accounts of vegetation in the Southern States have been published by Gano ('17), Harper ('13, '14, '20, '21, '27, '28), Mohr ('01), Small ('21, '22, '23, '25, '27), Wells, B. W., and Shunk, I. V. ('28, '31), and others. Each of these deals with a restricted area, usually one state or a portion of a state. This paper is an attempt to present a bird's eye view of the vegetation of the uplands of the lower Gulf Coastal Plain, commonly known as the longleaf pine belt, including parts of six states.

In view of the large number of plants indigenous to this region, only typical plants that are characteristic for certain conditions have been brought into the picture. Plants that have a wide distribution over the whole area east of the Mississippi River have been either omitted or given brief mention only.

The region described includes roughly the southeastern half of Georgia, the northern half of Florida, the southern half of Alabama, the southern half of Mississippi (excluding the Mississippi delta), the southern half of Louisiana, and the southeastern portion of the pine lands of eastern Texas. Consideration is given only to the vegetation of the rolling country, the flatlands, the upland stream margins, the shallow ponds and the swampy lands. The bottomlands of the principal rivers are omitted from discussion.

PHYSIOGRAPHICAL FEATURES OF THE GULF COASTAL PLAIN

The topography of the lower Gulf Coastal Plain ranges from level plain-like country along the gulf coast to gently rolling land rising gradually from sea level, increasing in altitude as it approaches the Piedmont Plateau and the Appalachian region. Altitudes vary from sea level to more than 600 feet. Toward the Mississippi River and the Gulf of Mexico, the elevation of the Gulf Coastal Plain decreases at the rate of about one foot per mile.

Late in the Tertiary period a blanket formation was deposited upon the coastal plain, known as the Lafayette formation. This is composed of a mantle of reddish or yellowish loams and sands frequently interspersed with beds of water-worn pebbles. The average thickness of the formation is about 25 feet. In many places this formation has been removed or is now being removed by erosion.

The flat areas along the gulf coast are poorly drained. There are many swampy depressions, in some of which the water table is near or above the surface, with the results that ponds and lakes are formed.

In the flat lands the principal soil types include the black soils of the Portsmouth series, the dark gray soils with mottled stiff clay subsoils of the Coxville series, the black soils with brown sandy "hardpans" of the St. Johns series, and the light gray soils with rusty brown sandy "hardpans" of the Leon series. The "hardpans" of the last-named series range in thickness from a few inches to a foot or more, and are located at depths of from 1 to 2 feet. They are characterized by high acidity and poor drainage.

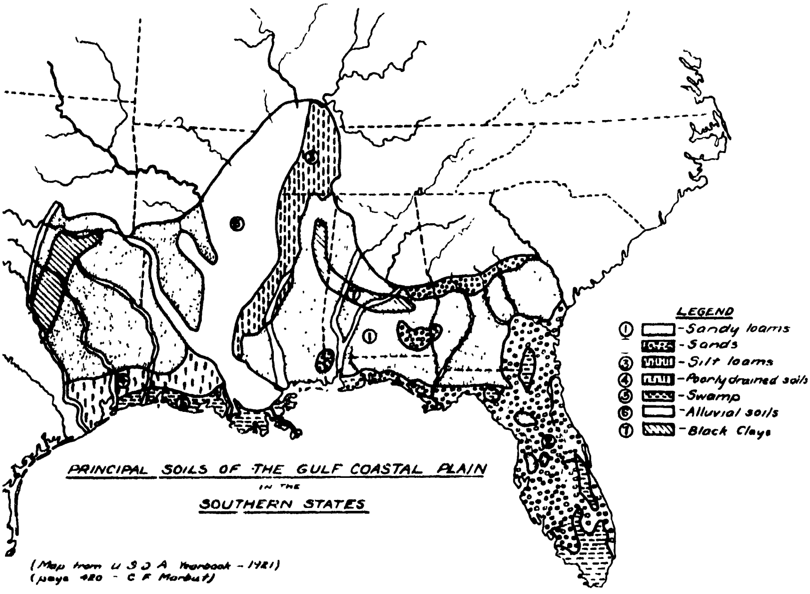

Fig. 1. Soil map of the Gulf Coastal Plain. After Marbut.

Farther inland the country is mostly rolling and, except for depressions, is well drained. Here the principal soils are the yellowish sandy loams of the Ruston and Norfolk series and the reddish soils of the Orangeburg and Susquehanna series. In the vicinity of the Mississippi River in Mississippi, Louisiana, and Arkansas the soil is almost entirely alluvial (fig. 1).

CLIMATE

The climate of the Gulf Coastal Plain is characterized by the absence of extreme temperatures. The mean annual temperature is about 67° F. The winters are short and mild. Although freezing weather is not unusual, the minimum temperature is 10° F. and this occurs rarely. For the winter months the average temperature is approximately 50° F. The summers are long and as a rule sultry, the relative humidity being high and the breezes light. The average summer temperature is about 85° F., although sometimes days occur with temperatures of more than 100° F. The actual percentage of sunshiny days averages from 40 to 60 in the winter and from 60 to 70 in the summer, spring, and fall. In winter the winds are commonly from the northwest, and in summer the prevailing winds are from the Gulf of Mexico. Annual rainfall for the whole area averages about 50 inches, and is rather evenly distributed throughout the year.

VEGETATION

The longleaf pine, *Pinus palustris* Miller, is the principal tree in the uplands of the lower Gulf Coastal Plain. Toward the northern margins of this zone it is replaced by loblolly and shortleaf pines as the predominant species. Unlike the other southern pines, longleaf pine tolerates a variety of habitats. It occurs on soils where the moisture is low, thrives on soils with an abundance of moisture, and is often found even on decidedly wet soils at the edges of ponds. It is unable, however, to withstand inundation over a long period of time. With the longleaf pine on the wetter sites is often associated the slash pine, *Pinus caribaea* Morelet. This species seems to be confined to moist sites and is often found in low depressions, where it frequently withstands inundation.

Although the climatic conditions are more or less similar throughout the Gulf Coastal Plain, the vegetation is not altogether uniform. It seems that edaphic conditions play a decided part in determining the character of the vegetation. On well-drained soils are found plant species entirely different from those inhabiting the poorly drained soils. Definite communities of plants occur along the borders of ponds and wet depressions that are decidedly different from those of higher ground.

FOREST ASSOCIATIONS

Although climatic conditions are more or less similar throughout the region, because of the diversity of the soils (especially in water-holding capacity) four distinct plant habitats are distinguished in the uplands of the Gulf Coastal Plain: (1) the sandy ridges, (2) the sandy flats, (3) the loamy flats and rolling country, and (4) the stream and pond margins. On the basis of these habitats and their distinct vegetation, five different forest associations are recognized: (1) the xerophytic deciduous forest, (2) the xerophytic coniferous forest, (3) the meso-hydrophytic forest, (4) the mesophytic coniferous forest, and (5) the hydro-mesophytic forest.

THE XEROPHYTIC DECIDUOUS FOREST

This is characterized by the scrub oak association composed principally of turkey oak, *Quercus catesbaei* Michx. (fig. 2). On the sandy ridges where this association occurs the sands are especially deep and the drainage rapid. This habitat is very dry. Whatever moisture reaches the soil as rainfall quickly percolates to the lower depths of the deep sands, beyond the reach of the roots of most plants inhabiting such soils. With the turkey oak on sandy ridges are commonly associated other scrub oaks of which post oak, *Q. stellata margaretta* Sarg., blue jack oak, *Q. cinerea* Michx., and live oak, *Q. virginiana geminata* Sarg., are typical examples. Longleaf pine is, also, a common associate. Sand pine, *Pinus clausa* Sarg., is confined mainly to sand dunes. The persimmon, *Diospyros virginiana* L., frequently occurs together with the oaks, but rarely develops into a tree of any size.

FIG. 2. Xerophytic deciduous forest, composed mainly of *Quercus catesbaei* Michx. A seedling of *Pinus palustris* Mill. is seen in the middle background.

One of the common shrubs is the scarlet balm, *Clinopodium coccineum* Kuntze. Haw, *Crataegus panda* Beadle, occurs abundantly and the gopher apple, *Chrysobalanus oblongifolius* Michx., literally covers the ground. Its rhizomes, located but one or two centimeters below the surface of the ground, spread underground for 10 meters or more, sending up aerial shoots at frequent intervals all along the length of stem. The haw, possessing a creeping root, spreads like the gopher apple.

Aristida purpurascens Poir is the predominant grass. The herbaceous plants are generally scattered, their density depending on the density of the oaks. Five species of legumes are always to be found on the sandy ridges. *Pitcheria galactoides* Nutt., is particularly abundant. A little less conspicuous is the devil's shoe-string, *Cracca spicata* Kuntze, which forms thick clumps occurring generally in open places in the forest. *Cassia chamaecrista* L. and *Morongia angustata* Britt. are scattered through the forest, but form a conspicuous component in this association. Another conspicuous plant is the dog's tongue, *Eriogonum tomentosum* Michx., which, although it does not occur in large clumps, is abundant on the sandy ridges and is easily noticed from early spring to late summer.

SUCCESSIONAL RELATIONS

The term "climax type" designates a stable type of forest produced in the succession of a plant community. This type is not subject to change (except through disintegration) so long as the general environmental conditions remain unaltered. "Sub-climax type" indicates the type that will exist as long as present biotic conditions prevail.

As to the successional stages in the xerophytic deciduous forest one can only theorize. Biotic factors have disturbed the vegetation in the days gone by, and may be expected to continue to do so. An opinion as to the possible aspect of this association in the distant future may not be out of place here.

Stands of virgin longleaf pine and scattered longleaf pine seed trees in the vicinity indicate that at one time longleaf pine was the predominant tree species on the cut-over areas now occupied by scrubby turkey oak. When the removal of the pines resulted in large openings permitting the sun's rays to warm the surface of the soil directly and to decrease the quantity of moisture in the soil, the turkey oak and other scrub oaks increased in number mainly because of their morphological adaptation to xerophytic conditions. The clear cutting of the pines also caused a considerable shortage of seed for the natural reproduction of the pines. Those pines that were left proved inadequate to restock the area. Longleaf pine seedlings that succeeded in establishing themselves soon perished either through drought, disease or through fires, which periodically burned over the cut-over land. Furthermore, the very slow growth of the longleaf pine seedlings during the first few years permitted the oaks to get a head start.

If the xerophytic deciduous forest is left undisturbed, that is, if it is protected from fire and other destructive biotic agencies, it may eventually be succeeded by a longleaf pine forest as a sub-climax type. If the scrub oak forest in its present state is left undisturbed there is a possibility, also, that in the far distant future the accumulated leaf litter of the oaks will improve the fertility and moisture-holding capacity of the soil to such a degree that mesophytic species can come in and take over the land, with the final result of a climax oak-hickory association. It is safe to assume that as long as present conditions prevail the present turkey oak-longleaf pine association will exist as a sub-climax type. In my opinion the xerophytic deciduous forest may change to the mesophytic climax forest (probably oak-hickory association) under complete fire protection or may return to the coniferous forest, even under conditions of periodic burning over of the land, if the supply of pine seed is adequate.

The question of the rôle played by fire in the succession of forest types deserves serious attention. My observation indicates that scrub oaks such as turkey oak, post oak, or blue jack oak are hardly ever killed out by surface fires in the south. Frequently the stems alone are killed or badly injured, the roots remaining uninjured, and in place of one destroyed stem the roots send up several new shoots with the result that consumption of water from the already impoverished soil becomes heavier and a keener competition arises between the pine seedlings and the oaks. The question of fire in relation to forest succession is an open one.

THE XEROPHYTIC CONIFEROUS FOREST

The forest association of the sandy flatwoods (fig. 3) in the lower Gulf Coastal Plain is composed mainly of longleaf pine. The soil of these flatwoods is predominantly sand with little or no underlying "hardpan." Although the land is flat, the drainage is good. The turkey oak, blue jack oak, and post oak occur in the openings and to some degree under the canopy of the pines. The black jack oak, *Q. marilandica* Muench., is sometimes found scattered under the pines. In addition to the scrubby oaks the gopher apple, *Chrysobalanus oblongifolius* Michx., the saw palmetto, *Serenoa serrulata*

FIG. 3. A typical view of the xerophytic coniferous forest. Scattered trunks of *Pinus palustris* Mill. are visible in the background. In the foreground are scrub oaks, principally *Quercus catesbaei* Michx., and clumps of *Serenoa serrulata* Hook.

Hook., and the scarlet balm, *Clinopodium coccineum* Kuntze, enter into the composition of this xerophytic pine forest. The herbs include principally *Pitcheria galactoides* Endl., the devil's shoe-string, *Cracca spicata* Kuntze, and *Cassia chamaecrista* L.

SUCCESSIONAL RELATIONS

Just as in the case of the xerophytic deciduous forest of the sandy ridges, the stages of succession of the vegetation on the sandy flatwoods is a matter of theory. This site seems somewhat more favorable for longleaf pine than the sandy ridges. Heavy cutting of the pines and periodic fires bring about a turkey oak association similar to the one produced on the sandy ridges. Judicious cutting with a certain degree of fire protection results in the longleaf pine sub-climax type. Some botanists and foresters hold that with complete fire protection those dry sandy flatwoods now dominated by scrub oaks would ultimately be dominated by longleaf pine, and the scrub oak associates would ultimately disappear from under the heavy canopy of the pines. It is my opinion that with complete fire protection the pines would predominate, but the scrub oaks would still form an important component, and that if the pines were removed the scrub oaks would predominate and ultimately there would develop an oak-hickory climax forest.

THE MESO-HYDROPHYTIC FOREST

In the moist sandy flatwoods where "hardpan" is frequent the soil is kept moist, owing to relatively poor drainage. In such areas longleaf pine predominates, but slash pine is often associated with it to such a degree that the association may bear the name of both tree species (fig. 4). Of particu-

FIG. 4. Typical meso-hydrophytic forest showing the intermingling of slash pine and longleaf pine and the abundance of the saw palmetto.

lar interest in such flatwoods are the tap roots of the pines. On reaching the "hardpan" the pine roots often fail to penetrate further but, twisting and turning, form short, stubby tap roots seldom more than 1½ meters in length (fig. 5). The pines in such flatwoods are generally much shorter than those inhabiting more favorable sites. The "hardpan," particularly common in the Leon series, is characterized by its high acidity. It is not definitely known whether the compactness of the "hardpan" layer, its high acidity, or improper respiration caused by poor drainage is mainly responsible for stunting the pines. The shallow-rootedness of the pines on such sites is certainly no special advantage, for the trees are easily thrown by wind.

FIG. 5. "Hardpan" layer in the Leon series showing the arrested root growth of a pine.

The shrubs most commonly observed in moist flatwoods are the saw palmetto, *Serenoa serrulata* Hook., the wax myrtle, *Myrica cerifera* L., the gallberry, *Ilex glabra* Gray, and a few species of *Hypericum*. These are excellent indicators of moist soil, being widely distributed on such soils through the lower Gulf Coastal Plain region.

In the hammocks in Florida the association is somewhat different. There *Magnolia grandiflora* L. and *Quercus laurifolia* Michx. predominate and their principal associates are *Q. nigra* L., *Q. virginiana geminata* Sarg., *Hicoria ashei* Sudw., *H. floridana* Sudw., *Tilia neglecta* Spach., and *Sabal palmetto* Roem. and Schult.

SUCCESSIONAL RELATIONS

The longleaf-slash pine association may be regarded as sub-climax. When moist sandy flatwoods are cut over and the areas subjected to periodic fires, sometimes an entirely different association results. The removal of the pines, and changes produced in the physical condition of the soil through burning, sometimes affect the drainage in such a way that the soil remains wet through most of the year. Often such areas develop into " pitcher-plant land " and are characterized by the predominance of *Campulosus aromaticus* Scrib. (the tooth-ache grass), *Xyris caroliniana* Walt., *Rhexia glabella* Michx., *Eriocaulon decangulare* L., pitcher plants, and lycopods. Such areas showing evidence of past pine stands abound in the Gulf States. Even the presence of seed trees does not often indicate the return of pines to these poorly drained lands. On many areas where the trees left after cutting might normally be sufficient to supply the necessary seed pine seedlings are nevertheless very scarce, the land being occupied largely by pitcher plants and lycopods. Especially is this true of areas located between ridges, for in such situations the moisture is considerably increased through run-off from adjacent higher ground. If subjected to unfavorable biotic conditions for many years it is possible that in the distant future wet sites now occupied by the meso-hydrophytic forest (the longleaf-slash pine association) may either become savannas or ultimately, if properly protected, become cypress-gum associations.

In Florida, however, slash pine often occupies ponds, growing on land that remains flooded for 15 months or longer.

THE MESOPHYTIC CONIFEROUS FOREST

The loamy flatwoods and rolling country of the lower Gulf Coastal Plain are characterized by moistness of the soil. Near the coast such habitats are generally occupied by longleaf pine. Farther inland longleaf pine has been replaced by loblolly pine on moist soils and by shortleaf pine on drier soils where the supply of longleaf seed is inadequate (fig. 6). With plenty of seed trees left after logging, not even fire prevents the natural reproduction of longleaf pine. Piney woods hogs, however, are very destructive to longleaf pine throughout the longleaf pine belt. The animals work on the roots of trees in the seedling and sapling stages, killing many and injuring many more.

On the sandy loams of the uplands of the lower Gulf Coastal Plain the characteristic tree associates of longleaf pine are the following: red gum, *Liquidambar styraciflua* L., southern red oak, *Quercus rubra* L., post oak, *Q. stellata* Wang., black jack oak, *Q. marilandica* Muench., and dogwood, *Cornus florida* L.

On moist soil bordering bay heads, springs, creeks, and ponds, longleaf pine gives way to slash pine, sweet bay, *Magnolia virginiana* L., and black gum, *Nyssa sylvatica* Marsh. The last mentioned species frequently appears as a pioneer on cut-over pine lands, and on moist sites frequently replaces not only longleaf pine but also loblolly pine.

On the drier soils horse sugar, *Symplocos tinctoria* L'Her, occurs more commonly than any other shrub. Species of *Crataegus* and *Vaccinium* are abundant. On slopes inclining towards wet depressions or bogs, wax myrtle and gallberry form sizable thickets together with species of *Rubus*. *Rhus vernix* L. is not uncommon along the margins of creeks.

FIG. 6. Typical second-growth longleaf pine forest on sandy loams in the lower Gulf Coastal Plain.

The herbaceous vegetation is composed mostly of grasses, of which species of *Andropogon*, *Muhlenbergia*, and *Aristida* are most conspicuous. Carpet grass, *Axonopus* sp., an introduced species, is very common but is confined largely to areas subjected to grazing. The genus *Panicum* is well represented on the sandy loams, as in other habitats of the region. The composites *Helianthus radula* T. and G. and *Solidago odora* Ait. are often conspicuous throughout the mesophytic coniferous forest, the former often crowding out grasses with its basal leaves closely pressing against the soil. *Drosera brevifolia* Pursh. abounds on the sandy loams, and serves as an excellent indicator of the moist character of the soil.

SUCCESSIONAL RELATIONS

Biotic factors that have been in operation in the past and that are likely to continue to operate make it impossible to predict with any degree of definiteness just what type of vegetation will occupy these flatwoods in the distant future. There is evidence that the hardwoods (oak-hickory) may ultimately take over the land if conditions for the coniferous forest become unfavorable either through heavy cutting or through some other factor. On the drier sites the tendency is for the southern red oak to take over the land, and on the moister sites the black and sweet gum enter as predominant species in the composition of the new association. On many moist sites inhabited by black gum and other moisture-loving hardwoods that have in recent years been protected from fires, the loblolly pine is coming back and forms large thickets. On such areas, also, it is not uncommon to see vigorous stands of young slash pine saplings. The tendency of the succession, however, is from the coniferous forest to the mesophytic deciduous forest, which if left undisturbed may eventually develop into a climax oak-hickory association, or, in the moister habitats, into a beech-magnolia climax association.

It must be emphasized that any prediction with reference to the climax vegetation on these flatwoods is purely theoretical.

HYDRO-MESOPHYTIC FOREST

There are numerous depressions in the flatwoods of the lower Gulf Coastal Plain, in which, owing to poor drainage, water stands for long periods of time (fig. 7). These depressions are inhabited by bald and pond cypress, *Taxodium distichum* Rich. and *T. ascendens* Brongn., together with black gum, *Nyssa biflora* Walt., and water gum, *N. aquatica* L. At the margins of such ponds one often finds red maple, *Acer rubrum* L., yaupon, *Ilex vomitoria* Ait., and other deciduous trees and shrubs. Where the land rises abruptly the surrounding country is usually inhabited by pines, principally slash pine (fig. 8); where the rise is gradual, the border country is generally marshy.

The cypress association is not entirely confined to depressions. It is often found occupying large tracts of flat land that are poorly drained and remain wet for long periods of time. Such areas abound in the vicinity of the gulf coast. Cypress is common, also, in the marshes bordering rivers. Species often found associated with it are *Chamaecyparis thyoides* B. S. P., *Nyssa aquatica* L., *N. ogeche* Marsh., titi, and red maple.

In the uplands swamp black gum, *Nyssa biflora*, occurs most commonly along the creeks and stream margins. With it are associated sweet bay, *Mag-*

FIG. 7. A typical cypress-gum association, showing the numerous pneumatophores of the cypress.

FIG. 8. Cypress-gum association in a depression in south Mississippi inhabited by pond cypress, *Taxodium ascendens* Brongniart, and black gum, *Nyssa biflora* Walt. Surrounding the depression are longleaf and slash pines.

nolia virginiana L., titi, *Cliftonia monophylla* Britt., sugarberry, *Celtis laevigata* Willde., and, to some extent, slash pine. Wax myrtle and gallberry generally abound on the higher ground bordering creeks. In the wetter places pitcher plants, lycopods, sphagnum moss, sedges, and *Myrica caroliniensis* Mill. predominate.

Successional Relations

The cypress-gum association is generally regarded as climax vegetation. Introduction of man's activities often completely alters this type of association. Drainage, especially, changes it entirely. On certain areas that have now been developed into agricultural lands and parks numerous stumps bear witness to a once magnificent stand of cypress.

Summary and Conclusions

1. The forest associations in the uplands of the lower Gulf Coastal Plain are determined largely by the prevailing edaphic conditions. On sterile, well drained, dry sands, after the longleaf pine has been removed, the typical xerophytic scrub oaks predominate, with *Quercus catesbaei* Michx. as the most common species.

2. On sandy flatwoods where " hardpan " commonly occurs longleaf pine, *Pinus palustris* Mill., and slash pine, *Pinus caribaea* Morelet, compose the forest association. Here the most common shrub associate is the saw palmetto, *Serenoa serrulata* Hook.

3. On the loamy flatwoods the longleaf pine is the predominant tree species. With it occur loblolly pine, *P. taeda* L., and shortleaf pine, *P. echinata* Mill. On the moister sites on these flatwoods longleaf pine is often replaced by loblolly pine; on the drier lands the southern red oak, *Quercus rubra* L., often follows longleaf pine, if the pine seed supply becomes inadequate. With an adequate supply of pine seed available the cut-over lands succeed in naturally restocking to longleaf pine, in spite of adverse conditions such as fire or grazing animals.

4. On the wetter soils in depressions or along streams and creeks, as well as on poorly drained flatwoods, the cypress-gum association predominates. This association may be surrounded by pines, where the land rises abruptly; where the land rises gradually, in general the border country is marshy and is inhabited by pitcher plants, sphagnum moss, lycopods, tooth-ache grass, and other marshy vegetation.

5. Some plants are excellent indicators of the wet or dry condition of the soil. The gopher apple, for instance, is an excellent indicator of dry soil, while such plants as the wax myrtle or gallberry appear to thrive best on moist soil, while pitcher plants indicate wet habitats.

6. In view of the diverse and complicated factors in operation, due almost entirely to biotic conditions, any attempt to explain and describe the climax vegetation in this large region must of necessity be purely theoretical. The preservation of areas in the wild state would yield further information with reference to the climax vegetation in this region.

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BIOLOGICAL CONDITIONS IN A PUGET SOUND LAKE[1]

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INTRODUCTION

The survey of Echo Lake, King County, Washington, as a biological habitat represents the first year-round investigation that has been carried out on a fresh-water body of the Pacific Northwest. It is hoped that this survey may form a basis of comparison with other lakes of the country, many of which have been studied in considerable detail. Several factors are suggested which might be primarily considered in a comparative study; namely: (1) geographical separation with resulting differences in the species of plants and animals present, and (2) climatic separation with resulting differences in the physical conditions of the water environment. It has been the aim of this paper to accurately portray biological and physical conditions in Echo Lake as being typical of several hundred shallow glacial pools scattered over the Puget Sound basin, all of kindred origin and subject to the same climatic influence.

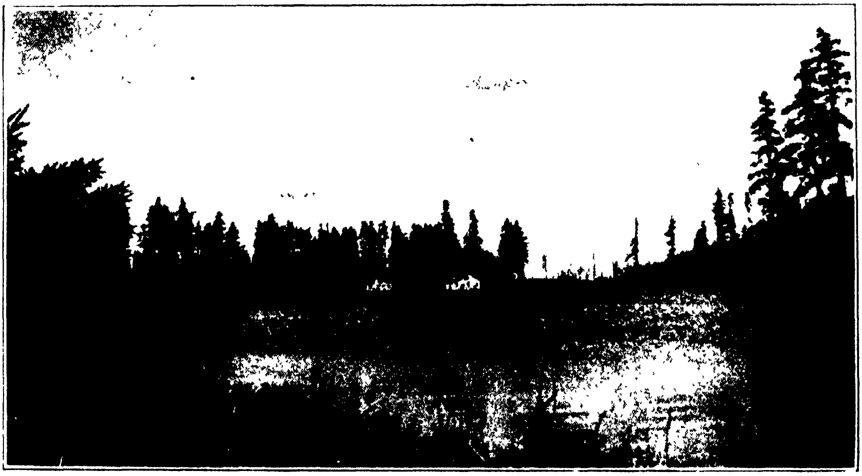

FIG. 1. Echo Lake.

Results of the survey may be summarized as follows: (1) An outline of the physiography of the region, (2) monthly records of physical and, to a limited extent, chemical conditions in the lake, (3) a quantitative analysis

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[1] A contribution from the Department of Zoology of the University of Washington.

of monthly variation in the abundance of plankton forms, and (4) a list of the dominant species of plants and animals present.

In order to obtain a general perspective of seasonal changes throughout the year, investigations were pursued over a period of thirteen months; November, 1930 to December, 1931. Monthly field trips were supplemented by laboratory work in the Zoology Department of the University of Washington.

PHYSIOGRAPHY

Echo Lake is located six miles north of Seattle in T. 26 N. R. 4 E.–S. 6. Roughly oval in shape, it covers an area of 56,330 sq. meters (13.9 acres) and is nowhere more than 10 meters deep. It rests in a shallow basin left in the glacial till by a retreating ice sheet which at one time extended some eighty miles south of Seattle (Bretz, '10, '11). During the late Pleistocene, the Vashon ice movement reached its maximum extent, and upon melting, a

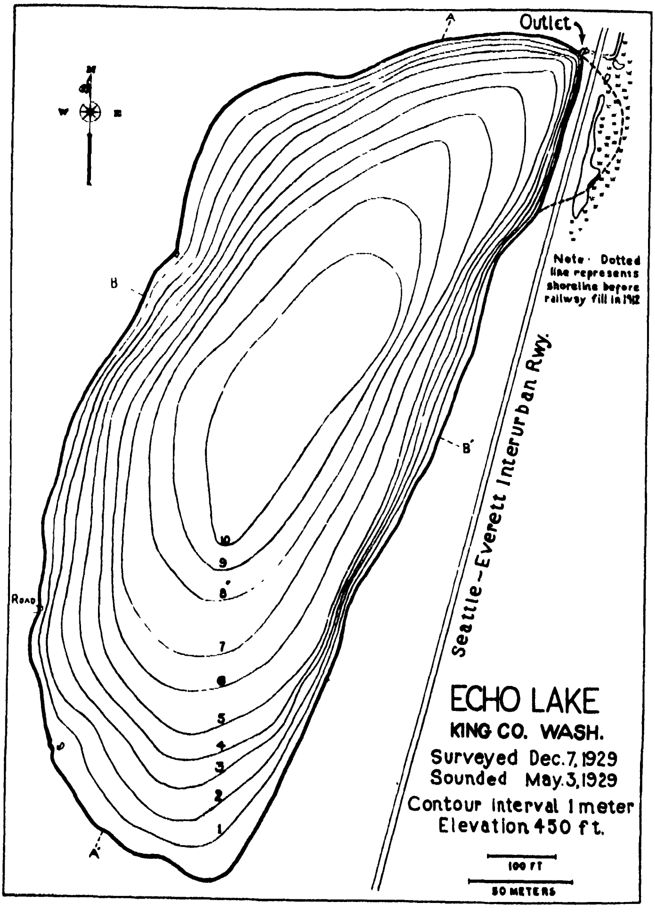

FIG. 2. Contour of Echo Lake.

hummocky sheet of dirt, sand, and water-worn boulders several hundred feet in thickness was left behind. The boulders are chiefly granite but many fragments of shale, schist, and volcanic rock are included. The underlying bedrock is seldom visible—only compact gravel, sand, and clay strata are exposed along the beaches of lakes scattered about on the till. Many shallow lakes have long since disappeared and others are dwindling because of floating vegetation which fills in from the edges and affords root for soil-building plants. This feature is noticeable at the shallower end of Echo Lake where the gently sloping bank has encouraged a growth of sphagnum moss.

The lake lies at an elevation of 450 feet above sea level among rolling, forest covered hills, and drains an area of approximately one square mile. Water enters the lake through several slow-flowing springs located in deep water near the center of the basin. When the lake level rises after the rains of early spring, water spills through the only outlet, a narrow culvert at the extreme northern end of the lake. Thence it travels through a meandering ditch for one and one-half miles to Lake Ballinger, and from here to Lake Washington which empties into Puget Sound through the ship canal. Reference to the water-level chart (fig. 3) will show that over a 13 month period, drainage through the culvert occurred for only four months, from February to May, 1931. The remaining drop in surface level was caused by evaporation during the summer months and by seepage through gravelly soil into nearby Lake Ballinger. Flood conditions occur in most of the Puget Sound lakes in early spring from March to April, for although the rainfall is not excessive, averaging 34.02 inches in Seattle, practically all of it occurs during the winter months. A contour map representing the results of sixty soundings illustrates the symmetrical nature of the water basin in Echo Lake (fig. 2). When the surface level was lowest at the close of summer in 1930, the

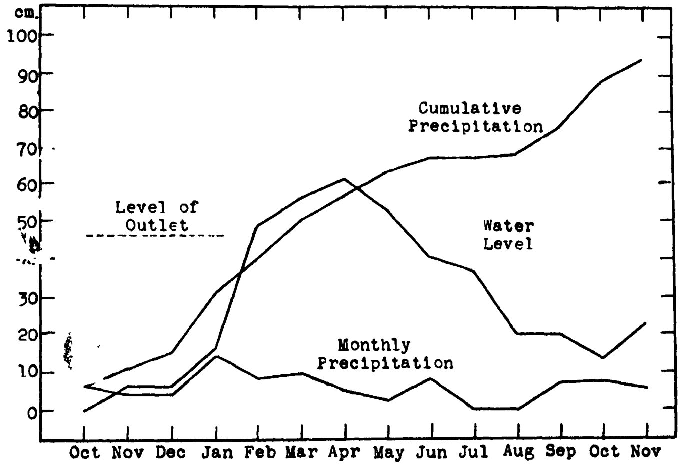

FIG. 3. Water level and precipitation in Echo Lake, 1930–1931.

volume of water was approximately 450,000 cubic meters, and when highest, in the spring of 1931, the volume rose to 485,000 cubic meters, or an increase of 7.8 per cent.

The shore line of the lake is regular, broken only by scattered clumps of willows and half-submerged logs jutting into the water. Vegetation typical of the humid Pacific Coast belt covers the banks. On a small inclosed lake of this type, wave action is not so powerful as to disturb the shore line, that is, to cut away semi-submerged vegetation or to deposit sandy beaches. The lake bottom is composed of soft black mud, interrupted in certain places near shore by boulders and sand. This mud is composed largely of decaying plant tissues, leaves, sticks, and silt, which when stirred give off the characteristic hydrogen sulfide odor of decaying organic material.

Physical and Chemical Conditions of the Water

Clarity

The water, like that of most of the other small lakes in the Puget Sound region, is fairly transparent. No silt bearing streams enter the lake and the only color is an amber tint in the depths; although at certain seasons the plankton may impart a definite hue to the water, as in September, 1931, when great masses of a blue-green alga (*Anabaena flos-aquae*) were taken in the net. As a standard to estimate light penetration in the water, the Secchi disc was used, values ranging from 5.6 meters in January to 3.1 meters in September, with a mean of 4.6 meters throughout the year. A careful consideration of both the factors involved in any change of the Secchi value, *i.e.*, atmospheric conditions and amount of suspended material in the water, reveals very clearly the fact that light penetration is affected more by the amount of plankton (especially phytoplankton) present than by cloudy weather or wind. Expressed mathematically, the volume of plankton per liter and the Secchi readings in Echo Lake for 1930–31 show an inverse rank correlation of 0.7, where 1.0 represents perfect correlation and 0 none.

Temperature

The water temperature chart (fig. 4) is self-explanatory in that it portrays monthly readings at one-meter depth intervals over a period of fourteen months. Generally speaking, the temperature was uniform at all depths in the five winter months from November to April, during which time it ranged from 9° C. to 4.5° C. Thus at no time did the water reach its point of maximum density. The formation of ice on Echo and similar lakes is commonly confined to an intermittent fringe around the shore; however about every third year the entire lake freezes over for a brief period of time. The formation of ice here can not be considered an important factor in plant and animal ecology, a feature which distinguishes the Puget Sound lakes from those of say, the Great Lakes region. From April the surface waters warmed *to a maximum in July and dropped back to a uniform level in November. During the warmer months a definite thermocline or discontinuity layer appeared between the upper and lower water strata. Its position lay at a depth of three meters below the surface in May and descended almost exactly one meter per month until it reached the bottom in November, coincident with the autumnal mixing of all water layers.* A point of interest in this temperature chart is the "lag" or inertia of the lower strata as compared with the upper; that is, the order in which each stratum, surface, middle, and bottom, attained its highest temperature was, respectively, July, September, and October.

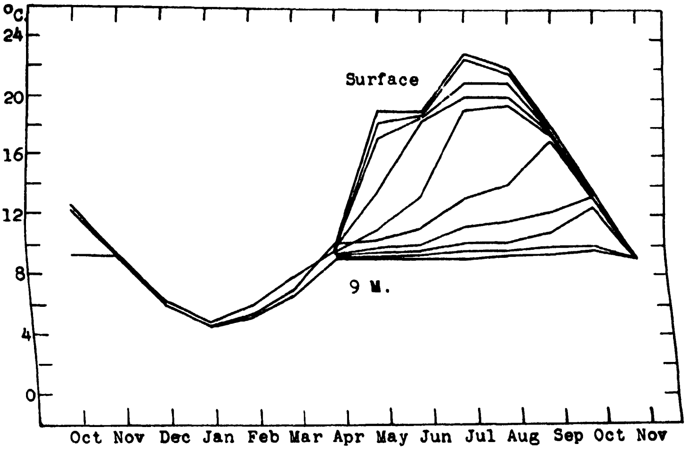

FIG. 4. Temperature of the water in Echo Lake, 1930–1931.

Dissolved Oxygen

Of all dissolved gases in lake water, probably the one of greatest biological significance is oxygen. In Echo Lake, definite stratification of the

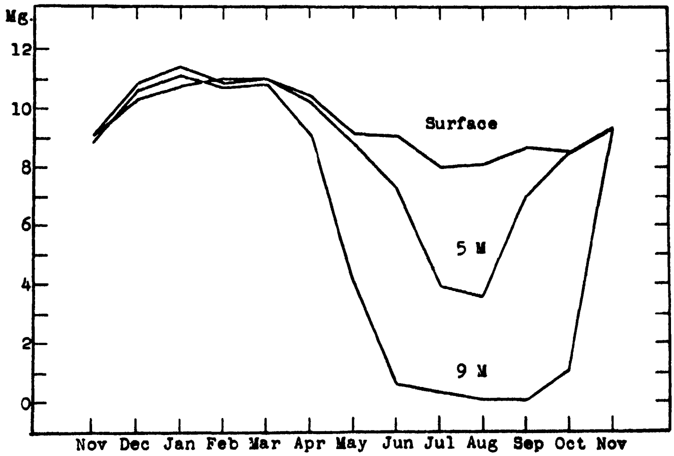

FIG. 5. Dissolved oxygen in Echo Lake, 1930–1931.

water according to its oxygen content was evidenced during the warm months of April to October (fig. 5). At about the middle of this period, in August, the surface waters held 8 mg. per liter, the middle depth half this amount, and the bottom none at all. The presence of hydrogen sulfide, as revealed by its odor, explains the absence of oxygen near the lake bottom during those months when organic decomposition was progressing most rapidly.

Acidity

The water in Echo Lake at all levels was acid in reaction throughout the year with the exception of the surface which approximated neutrality during the summer months (fig. 6). The greatest recorded acidity was pH 5.8, caused by hydrogen sulfide, carbon dioxide, and organic acids near the lake bottom in June. Circulation of the water in January through the prolonged action of the wind produced uniform conditions at all depths, not only as regards pH but also temperature and dissolved oxygen.

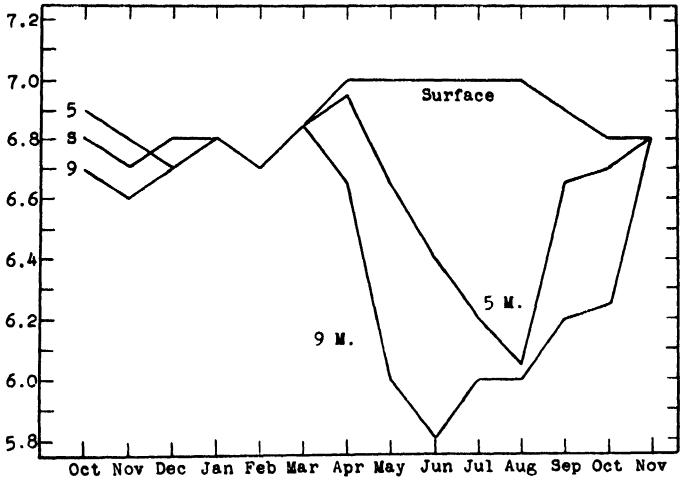

FIG. 6. Hydrogen ion concentration in Echo Lake, 1930–1931.

SHORE AND BOTTOM LIFE

The area surrounding the lake has been referred to as wooded. Conifers, deciduous trees and shrubs are densely intermingled, the total effect being to conserve rainfall which ultimately drains into the lake. The author feels that the deciduous trees are also important in their relation to aquatic productivity, that is, the wind-blown leaves and detritus contribute to the stock of organic food material and mineral salts in the water. A list of the prominent species of trees and shrubs includes (Frye, '14): *Pseudotsuga taxifolia* (Douglas Fir), *Thuja plicata* (Western Red Cedar), *Tsuga heterophylla* (Western Hemlock), *Acer macrophyllum* (Large-leaved Maple), *Acer* *circinatum* (Vine Maple), *Alnus oregona* (Red Alder), *Cornus nuttalii* (Flowering Dogwood), *Corylus californica* (Hazel), *Populus balsamifera* (Balm-of-Gilead), *Salix* sp. (Willow), *Spiraea corymbosa* (Spiraea).

At the northern extremity a railroad fill constructed 20 years previous to the time of this survey has isolated a small body of water now become boggy in nature. Plants found here are: *Comarum palustre* (Purple Marsh-Locks), *Drosera rotundifolia* (Sundew), *Kalmia polifolia* (Swamp Laurel), *Ledum groenlandicum* (Labrador Tea), *Sphagnum* sp. (Sphagnum), *Spiraea douglasii* (Hardhack).

On many occasions animals have been observed in and along the edges of this bog, amphibians especially finding the warm, quiet water suitable for egg laying (Slevin, '28): *Triturus torosus* (Escholtz) (Pacific Coast Newt), *Ambystoma paroticum* Baird (Northwestern Salamander), *Hyla regilla* Baird and Girard (Pacific Tree Toad), *Rana pretiosa pretiosa* (Baird and Girard) (Western Spotted Frog), *Bufo boreas boreas* (Baird and Girard) (Northwestern Toad), and also: *Thamnophis ordinoides ordinoides* (Baird and Girard) (Puget Garter Snake), *Microtus townsendi* (Meadow Mouse), *Sorex vagrans vagrans* (Wandering Shrew).

Marginal vegetation along the lake shore, while not abundant, includes the following: *Hypericum anagalloides* (St. John's Wort), *Nymphaea polysepala* (Yellow Water Lily), *Castalia* sp. (White Water Lily), *Typha* sp. (Cat-Tail), *Paspalum distichum* (Joint Grass).

Throughout the entire year, but especially during cold, sunny periods in early spring, masses of algae collect in the quiet inlets among emergent grass blades and cat-tail stalks. This type of situation affords protection for a fauna and flora quite different from that of the plankton. The plants are chiefly represented by filamentous algae, diatoms, and desmids; while living on or among these are many types of animals. A complete list of organisms identified may be found at the end of this paper, but in brief, the most conspicuous animals are the amphipods, snails, insect larvae, beetles, mayflies, dragon-flies, damsel-flies, and caddis-flies.

The lake bottom is composed almost entirely of soft, brownish black mud, a habitat which might appear at first glance unfavorable to the growth of molluscs. However, in the shallower water where a certain amount of sand is present, two Sphaeridae are encountered: *Pisidium pilula* Sterki and *Sphaerium patella* Gould. Three insect larvae are also commonly seen in this situation: *Donacia proxima* var. *californica* (on Nymphaea roots), *Eristalis* sp., and *Chironomus* sp.

THE PLANKTON

Emphasis has been placed on the study of microscopic life in the open waters of Echo Lake. Qualitative plankton hauls taken each month of the survey were supplemented by tows taken at irregular intervals in past years. In addition, measured volumes of water from each of four depths were subjected to a quantitative analysis of the net plankton present. Results of an examination of these samples have been shown graphically in figs. 7 to 9 and table I, while general notes on the plankton are as follows:

(1) The summer plankton is characterized by a greater variety of species than is the winter, that is, an average collection in August will contain about 25 forms as compared with 10 for January. The total number of limnetic

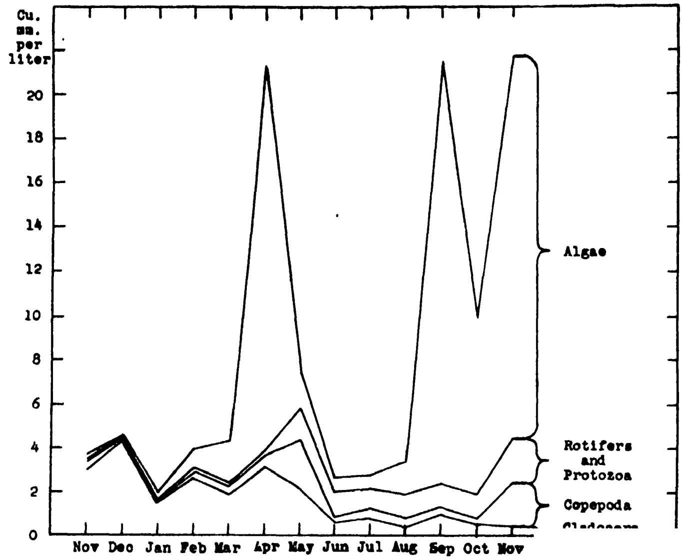

FIG. 7. Total volumes of net plankton in Echo Lake, 1930–1931.

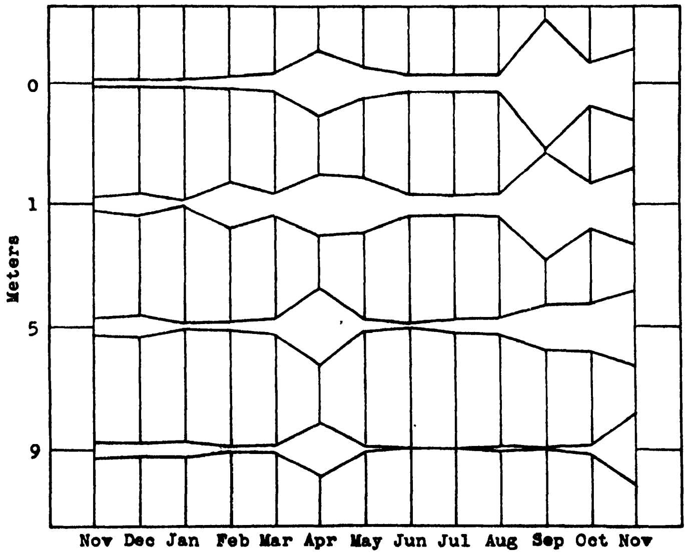

FIG. 8. Seasonal distribution of net plankton in Echo Lake, 1930–1931.

species observed over a 13 month period approximates 75, distributed as follows: Cyanophyceae (6), Baccilariaceae (6), Chlorophyceae (35), Mastigophora (5), Infusoria (2), Rotifera (10), Cladocera (6), Copepoda (2), Insecta (1).

(2) Great irregularity is shown in the total volume of plankton present in different months of the year, apparently not correlated with a disturbance of the physical condition of the water in as great a degree. A sudden rise in the volume is invariably due to the rapid growth of one or more species of microscopic plants. In April, a sharp peak in the plankton volume was caused by the appearance of *Volvox* colonies; in late summer by *Anabaena* and *Botryococcus* in such numbers as to impart a greenish cast to the water. The volume of algae present in November, 1931 was approximately *250 times* that of November, 1930.

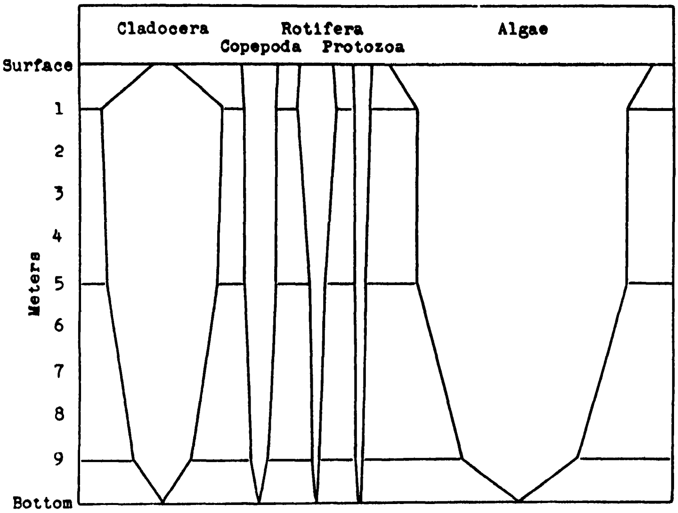

FIG. 9. Vertical distribution of net plankton in Echo Lake, 1930-1931.

(3) During the summer months, horizontal stratification of the plankton occurs simultaneously with that of the temperature, pH, and oxygen content. Deficiency of oxygen at 9 meters brings an absence of practically all life (excepting the midge larva *Corethra*) during the six months from May to October (fig. 8). The shells of dead organisms such as *Anuraea*, *Notholca*, desmids and diatoms are not uncommon at 9 meters, these apparently having settled from the upper waters.

(4) The volume of plankton is slightly greater at a depth of one meter than at the surface. Individual organisms, however, have their maxima at different levels (fig. 9).

(5) Larvae of the midge *Corethra* were found in quantitative plankton hauls in nearly every month of the year, varying in numbers from 125 per

TABLE I. *Occurrence of prominent plankton organisms in Echo Lake, 1930–1931*

	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.
Anabaena.........							+	+	500,000,	45,000	24,000,000	+	+
Aphanizomenon....							+	400,000	330,000	52,000	50,000	60,000	+
Fragilaria.........	+	+	+	+	+	+	+	+	+	1,500	106,000	630,000	15,500
Asterionella........	+	+	+	8,000	120,000	1,022,000	20,000	+	+	3,100	11,000	9,000	29,000
Sphaerozosoma.....					40		+		1,300		3,900		2,100
Eudorina..........	11	21	54	470	1,470	4,100	690	630	340	1,400	2,300	300	630
Volvox............	+	1.5	2.4	3.5	9	600	+	+	+	4	25	85	4.5
Botryococcus.......	60	11	23	2	15	25	80	100	210	2,100	18,000	12,000	27,000
Dinobryon.........	+					+	48,000	2,100	4,200	30,000	66,000	2,200	500
Peridinium........	+	+	28	54	92	+						+	+
Ceratium..........	+				7	+	40	100	+	72	210	140	+
Carchesium........	5	1	+	+							250	140	400
Polyarthra...... ...	+				+		26	130	370	150	82	50	2
Anuraea..........				+	+	+	+	+	400	240	+	50	+
Notholca..........										+	370	240	600
Conochilus.........	4	+				+	530	220	+			+	
Daphnia..........	2.4	16	1.6	5.8	13	1.5	.9	.7	.7	.1			+
Bosmina..........									60	23	+	+	.9
Ceriodaphnia.......							+			1.6	29	12	5
Diaptomus.........	1.2	1.2	3.6	4.9	8.4	20.9	21.7	5.4	5.8	9.5	5.6	4.6	50.2
Corethra...........	.15	.19	.19	.24	.55	.18	.21	.11	.05	.45	0	.01	0

Explanation

Numbers represent individuals per liter (colonies in the case of *Volvox, Eudorina,* and *Botryococcus;* cells in other algae).

Plus mark signifies present in small numbers only.

Months of maximum abundance underlined.

Plankton counts from the 9 meter samples of May–September are not included in this table, since this stagnant water does not contain a representative plankton during the summer.

50 liter sample (March, 9 meters) to none at all in September and November, though their absence from the samples of these last two months was possibly accidental. While most abundant near the lake bottom, the larvae ranged into the upper waters during the winter. In the seven warmer months from May to November they were never taken above 5 meters. Observations of *Corethra* at five widely separated dates in 1931 give a basis for the provisional conclusion that the adults emerge in successive generations from March 15 to September 15. Muttkowski ('18) found *Corethra punctipennis* emerging from Lake Mendota in three generations from May to September.

(6) Considerable amounts of organic debris, largely fragments of plant tissues, are present in the fall and winter months. Part of this material is wind-blown and part stirred up from the oozy lake bottom by wave action. Here must be a valuable source of food for water bacteria and lower plants which, in turn, are eventually eaten by the larger plankton.

(7) Littoral and limnetic plankton regions are well defined, even on a lake as small as Echo. Only occasionally are shallow water forms (such as *Canthocamptus staphylinus* and *Cyclops serrulatus*) taken in mid-lake.

(8) A succession of the species of Cladocera present throughout the year has been observed on Echo and other small lakes in the vicinity of Seattle. Two species of *Daphnia* are almost invariably the chief representatives of the Cladocera in Echo Lake, but in July, 1931, *Bosmina* gradually assumed the position of major abundance, only to give way to *Ceriodaphnia* in the late summer. In the spring of 1932, a plankton haul revealed *Daphnia* once more abundant and no sign of the other forms (table I).

ECONOMIC CONSIDERATIONS

Coincident with the growing population of the Pacific Northwest in the past twenty years there has come a development of the suburban areas around the larger cities. This has brought an increased valuation to the score of small lakes which are located in the vicinity because of their greater possibilities as recreational centers. Many lake owners have chosen to build permanent homes along the water, while others have commercialized their property by erecting facilities for public camping, fishing, boating, and bathing. Year by year the influence of man is becoming more evident in the alteration of each lake as a biological habitat. A typical example of this may be seen in Echo Lake where several changes have been brought about through attempts to increase its value as a recreational center, namely by the introduction of fish and by the chlorination of bathing beaches as a sanitary measure. Fish are not as plentiful as they were twenty years ago; but of course this condition exists in all lakes near the larger cities. Through the efforts of the King County Game Commission, five plantings of fish have been made in Echo Lake with stock seined from a productive body of water lying within the city limits, Green Lake, as follows: 10,000 Black Bass (1912), 8,000 Perch (1915), 20,000 Black Bass (1927), 10,000 Black Bass (1928), 15,000 Black Bass (1930).

Although it was the intention to stock only bass and perch, some crappies have undoubtedly been introduced as well, since these are present in both lakes. The introduction of trout as game fish might be suggested by a consideration of the abundance of plankton food in Echo Lake, but on the other hand, it is doubtful whether the oxygen content of the cool hypolimnion would be sufficient to support their existence during the summer.

A minor disturbance of the plankton life was occasioned in August, 1931 by chlorination of water along the bathing beaches. During investigations by the King County Health Department as to sanitary conditions in public resorts, a series of water samples were taken from Echo Lake for bacterial analysis. In addition, the author collected two samples which were examined by the City authorities. A report on these findings is as follows:

October 15, 1930: Bacteria count per cc. (37° C.)—3, *B. coli* group per 100 cc.—0.

July 13, 1931: Bacteria count per cc. (37° C.)—99, Bacteria count per cc. (20° C.)—500, *B. coli* group per 100 cc.—4.

August 8, 1931: Bacteria count per cc. (37° C.)—26, Bacteria count per cc. (20° C.)—250, *B. coli* group per 100 cc.—4.

November 14, 1931: Bacteria count per cc. (37° C.)—26, Bacteria count per cc. (20° C.)—10,000, *B. coli* group per 100 cc.—2.

These figures show a slight increase in the number of mesophilic (37° C.) bacteria during the warm summer months, and also suggest that in November, 1931 a great increase in the number of soil and water bacteria attended the heavy rains of this season.

According to a standard adopted by the Public Health Service (Washington, '21), water to which the public has access should not contain more than 100–37° C. bacteria nor more than 2 *B. coli* per 100 cc. On July 15, therefore, Echo Lake was condemned as unsafe for public use and two property owners who operate swimming resorts along the beach were ordered to sterilize the water by means of chlorination. Three chlorinations were made along the beaches, on August 8th, 17th, and 22d, the operations being carried out from a light motorboat which circled the bathing area. A trade solution of sodium hypochlorite ("Clorox," 4.5 per cent Cl) was used, and each quart of stock liquor calculated to sterilize 32,000 gallons of water.

As to the value of such treatments in reducing the bacterial count, little can be said, since the Health Department failed to take water samples following chlorinations. However, on August 17th, four hours after two quarts of Clorox had been administered, all copepods observed in a surface tow near shore were lifeless, and it follows that the bacteria would also have been killed. Plankton organisms in mid-lake were not noticeably affected by the chlorine, since it was applied only in the bathing area. The effect of chlorine on fish life, especially the young fry which gather in shoal water along the beaches, has been decried by Seattle sportsmen. Considering the value of Echo and other suburban lakes from a broad viewpoint, however, there is no question but that the fullest benefits will be derived from their use as public bathing resorts and, of necessity, sanitary measures introduced which will tend to check the growth of fish life.

METHODS AND APPARATUS

Water temperatures were taken with an Eckmann reversing thermometer and air temperatures with a Tycos nitrogen filled thermometer, both instruments reading in tenths of a degree Centigrade. Water samples were collected in a ten liter closing bucket similar to that described by Bajkov ('29, p. 346) and the dissolved oxygen content estimated by the Winkler process (A. P. H. A., '25). Tests on two occasions showed that the Rideal-Stewart modification was unnecessary, as might be expected in water free from pollution. Several points of procedure were adopted from a report of the U. S. Bureau of Fisheries (Kemmerer, '23); namely the use of a standard solution of potassium dichromate (N/100) and Low's starch solution as an indicator.

Determination of the hydrogen ion concentration was made in the field by the colorimetric method, using a Hellige-Klett comparator disc with bromthymol blue or bromcresol green (A. P. H. A., '25). Although the figures on this apparatus are marked only in intervals of pH 0.2 (as 6.2, 6.4, etc.) it is quite possible to estimate readings in steps of 0.05.

The technique of quantitative plankton sampling was adopted with modifications from Bajkov ('29). The use of a fairly large closing bucket suggested itself as combining the features necessary in water sampling for both plankton and chemical analysis. A ten-liter galvanized cylinder was constructed with hemispherical rubber-lined valves opening upward on top and bottom. After being dropped to the desired depth, an upward pull closes the valves and prevents contamination of the sample by water from upper strata. A can of this capacity is easily transported and easily handled without a boom in the boat. When dropped, the can is flushed thoroughly and cuts off quickly a definite volume of water. By the addition of a short length of tubing to a petcock set in the can, samples of water for chemical analysis may be run out without contact with the air, and thus the can made to serve a dual purpose.

Quantitative samples were taken from an identical position in mid-lake each month, with the boat anchored to a small buoy, except in the case of surface plankton samples which were taken as the boat drifted along, in order to have undisturbed water for each. Fifty liters of water (five buckets) were poured through a No. 20 silk net and the catch preserved in 4 per cent formalin.

Enumeration of organisms in the net plankton was accomplished with the aid of a Sedgwick-Rafter counting cell and an ocular micrometer (A. P. H. A., '25). By this method both the numbers and size of each organism were recorded. One count was made from each sample save that the Cladocera and Copepoda were counted in two lots, since their distribution on the slide is apt to be less uniform. Crustacea and rotifers of varying ages (and hence sizes) were estimated accordingly. Such photosynthetic forms as *Volvox* and *Dinobryon*, though commonly considered flagellates, were classed as algae. Corethra larvae were not included in volumetric plankton tables because their relatively great size would cause them to bear undue weight in the compilation of total volumes. In tabulating the results of plankton counts many items have been grouped in large classes to express general relationships and to minimize the errors which undoubtedly occur in individual counts. Figures 7, 8, and 9 represent unit volumes of plankton as square units on paper.

List of Species[1]

Cyanophyceae: *Aphanothece prasina* A. Braun, *Coelosphaerium naegelianum* Unger, *Oscillatoria* sp., *Lyngbya limnetica* Lemmermann, *Anabaena flos-aquae* (Lyng.) Bréb., *Aphanizomenon flos-aquae* Ralfs.

Chlorophyceae: *Melosira crenulata*, *Diatoma* sp., *Fragilaria* sp., *Asterionella gracillima* Heiberg, *Tabellaria fenestrata* Kützing, *Hyalotheca dissiliens* (Sm.) de Bréb., *Sphaerozosoma* sp., *Desmidium aptogonium* de Brébisson, *Desmidium swartzii* C. A. Agardh. *Closterium subtruncatum* W. and G. S. West, *Closterium acutum* (Lyngbye) de Bréb., *Closterium ralfsii* de Brébisson var. *hybridum* Rabenhorst, *Closterium leibleinii* Kütz., *Closterium kützingianum* de Brébisson, *Closterium costatum*, *Closterium gracile* de Brébisson, *Closterium* sp., *Spirotaenia condensata* de Brébisson, *Pleurotaenium trabecula* (Ehrenb.) Nägeli, *Staurastrum dejectum* de Brébisson, *Staurastrum dickei* Ralfs. var. *maximum* W. and G. S. West, *Staurastrum paradoxum* Meyen and var. *longipes* Nordstedt., *Staurastrum chaetoceros* (Schroeder) Smith, *Staurastrum furcigerum* de Brébisson, *Staurastrum arctiscon* (Ehrenb.) Lundell, *Micrasterias sol* var. *ornata* Nordst., *Micrasterias americana* (Ehrenb.) Ralfs, *Euastrum verrucosum* var. *alatum* (Ehrenb.) Wolle, *Cosmarium bioculatum* de Brébisson, *Cosmarium botrytis* (Bory.) Menegh., *Cosmarium reniforme* (Ralfs) Arch., *Cosmarium quinarium* Lund., *Cosmarium tumidum* Lund., *Cosmarium contractum* Kirchn., *Cosmarium pseudonitidulum* Cooke, *Arthrodesmus incus* (de Bréb.) Hass, *Xanthidium subhastiferum* W. West, *Zygnema* sp., *Spirogyra* sp., *Mougetia* sp., *Pandorina* sp., *Eudorina elegans* Ehrenberg, *Volvox aureus* Ehrenberg, *Tetraspora lacustris* Lemmermann, *Botryococcus brauni* Kützing, *Oocystis borgei* Snow, *Ankistrodesmus falcatus* (Corda) Ralfs, *Quadrigula pfitzeri* (Schröder), *Characium* sp., *Scenedesmus obliquus* (Turpin) Kützing, *Scenedesmus dimorphus* (Turpin) Kützing.

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[1] The author is greatly indebted to the following fellow-workers for kind assistance in identification; G. H. Wailes (Desmidaceae), Marjorie Wells (Trichoptera), Elsa Thorstensen (Amphipoda), Melville Hatch (Coleoptera), Guinivere Storey (Ephemerida), Junius Henderson (Mollusca), Hortense Lanphier (Hemiptera), Leonard Schultz (Pisces).

Sarcodina: *Amoeba proteus* Leidy, *Arcella vulgaris* Ehrenberg, *Centropyxis* sp., *Difflugia globulus*, *Trinema enchelys* Ehrenberg, *Acanthocystis penardi* Wailes.

Mastigophora: *Euglena* sp., *Mallomonas caudata* Iwanoff, *Synura uvella* Ehrenberg, *Dinobryon sertularia* Ehrenberg, *Dinobryon cylindricum* var. *palustre* (Lemm.), *Peridinium willei* Huitf-Kaas, *Peridinium tabulatum* (Ehrenberg), *Ceratium hirundinella* Müller.

Infusoria: *Tintinnidium fluviatilis* Stein, *Carchesium epistilides*.

Porifera: *Spongilla lacustris* (Linnaeus).

Hydrozoa: *Hydra viridissima* Pallas, *Hydra oligactis* Pallas.

Platyhelminthes: *Planaria maculata* Leidy, *Dendrocoelom lacteum* Oersted.

Rotatoria: *Polyarthra platyptera* Ehrenberg, *Rattulus* sp., *Anuraea cochlearis* Ehrenberg, *Notholca longispina* Kellicott, *Notholca* sp., *Ploesoma* sp., *Asplanchna* sp., *Conochilus volvox* Ehrenberg.

Oligochaeta: *Xironogiton oregonensis* Ellis.

Cladocera: *Sida crystallina* (O. F. Müller), *Holopedium gibberum* (Zadach), *Daphnia pulex* (de Geer), *Daphnia longispina* (O. F. Müller), *Simocephalus serrulatus* (Koch), *Ceriodaphnia quadrangula* (O. F. Müller), *Bosmina obtusirostris* Sars, *Chydorus sphaericus* (O. F. Müller).

Copepoda: *Diaptomus shoshone* Forbes, *Diaptomus washingtonensis* Marsh, *Cyclops albidus* Jurine, *Cyclops serrulatus* Fischer, *Canthocamptus staphylinus* Pearse.

Ostracoda: *Cypridopsis vidua* O. F. Müller, *Cypris* (*Cypris*) *testudinaria* Sharpe.

Amphipoda: *Eucrangonyx gracilis* (Smith).

Decapoda: *Potamobius trowbridgii* Stimp.

Ephemerida: *Blasturus cupidus* Say, *Callibaetis fusca* Dodds.

Hemiptera: *Gerris buenoi* Kirkaldy, *Gerris rufoscutellatus* Latreille, *Gerris marginatus* Say, *Notonecta vulnerata* (Uhler), *Notonecta laevigata* (Uhler), *Notonecta undulata* Say, *Notonecta insulata* Kirby.

Trichoptera: *Halisochila taylori*, *Limnephilus* sp.

Coleoptera: *Acilius semisulcatus* sub. *abbreviatus* Aube., and ab. *latuisculoides* Hatch, *Agabus discors* Lec., *Agabus anthracinus* Mann., *Agabus lutosus* Lec., *Agabus strigulosus* Cr., *Agabus tristis* Aube., *Anacaena limbata* F., *Berosus striatus* Say, *Bidessus affinis* Say and var. *microreticulatus* Hatch, *Coelambus columbianum* Brown, *Coelambus punctatus* Say, *Coelambus obscureplagiatus* Fall, *Coelambus hydropicus* Lec., *Colymbetes exaratus* Lec., *Cymbiodyta acuminata* Fall, *Donacia proxima* var. *californica* Lec., *Dytiscus sublimbatus* Lec., *Gyrinus latilimbus* Fall, *Gyrinus maculiventris* Lec., *Gyrinus picipes* Aube., *Haliplus immaculicollis* Harr., *Helophorus tuberculatus* Gyll., *Helophorus* (s. str.) *linearis* Lec., *Helophorus* (s. str.) *inquinatus* Marn., *Hydrobius fuscipes* L. and abb. *rottenbergi* Gerh., *Hydrochus excavatus* Lec., *Hydroporus consimilis* Lec., *Hydroporus terminalis* Sharp, *Hydroporus* (s.

str.) *humeralis* Aube., *Hydroporus striatellus* Lec., *Hydroporus* (s. str.) *striola* Gyll., *Laccophilus decipiens* Lec., *Laccobius ellipticus* Lec., *Rhantus binotatus* Harr., *Tropisternus lateralis* var. *dorsalis* Br., *Tropisternus columbianus* Brown.

Diptera: *Corethra* sp.

Mollusca: *Pisidium pilula* Sterki, *Physa ampullacea* Gould, *Planorbis* sp. (similar to *antrosus*), *Sphaerium patella* Gould, *Ferrissia caurina caurina* (Cooper).

Pisces: *Aplites salmoides, Pomoxis sparoides* (Lacepede), *Perca flavescens* (Mitchill).

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A DETAILED STUDY OF DESERT RAINFALL

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It is well known that the precipitation that falls during a given rain is not uniform throughout the area covered by the storm. A desire to obtain a better knowledge of these variations in a desert climate and their possible effects on vegetation prompted this study.

The only previous investigation of rainfall differences on a small area that has come to my attention is one carried out by Musson ('03) near Windsor, New South Wales. In this work 47 gauges were placed in the form of a cross 1 mile long and readings were taken after each shower for three months. The highest readings in this series were from 25 per cent to 30 per cent greater than the lowest readings. The author concludes that variations of 20 per cent or more may be expected in the precipitation falling on a single square acre.

In August, 1930, a series of 24 rain gauges was installed on the grounds of the Desert Laboratory. Sixteen were placed in four rows of four gauges each at intervals of 100 m., thus occupying a square 300 m. on a side. This square was located on the level ground immediately west of Tumamoc Hill. Eight additional gauges were placed in a straight line at 100 m. intervals from the east corner of the square toward the base of Tumamoc Hill and up its slopes to a spot 200 meters above its base (fig. 1).

A type of gauge was used that consisted of a galvanized iron funnel topped by a vertical collar 5 inches high, inserted through a cork in the top of a quart mason jar. An instrument of this same general type was used by Shreve ('15) in his studies in the Santa Catalina Mountains of Arizona, and by Cooper ('17) in a study of precipitation in redwood forests. The gauges used by Cooper had metal rather than glass containers, but were otherwise rather similar.

The water was poured from the jar in which it collected into a graduate and this volume was converted into depth of precipitation by dividing the volume of water by the area of the mouth of the funnel.

The period of observation included all the rains that fell within the year from August 28, 1930, to August 28, 1931, and includes 48 periods of precipitation. Readings were made immediately after every rainfall.

It may be well to mention briefly the salient features of the rainfall in the Tucson region. There are two principal periods of precipitation, one usually occurring during the summer months from late June through July and August, and the other falling in the winter months during the period

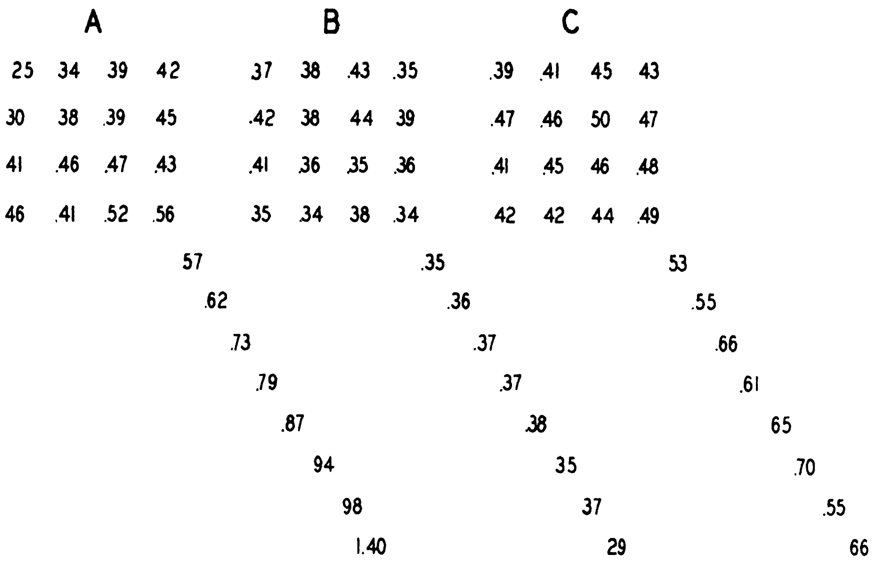

FIG. 1. Rainfall records in inches showing also the relative position of the rain gauges: *A*. Rain of August 3, 1931, a summer storm; *B*. Rain of November 14, 1930, a typical winter rain; and *C*. Rain of July 13, 1931, a typical summer rain.

from November to late February or early March (fig. 2). Relatively insignificant showers, falling at infrequent intervals, may occur at any time during the intervening dry seasons. The winter precipitation is usually gentle, ranging from a mist to a definite steady rain, and is often relatively long in duration. Only infrequently, however, does it continue without cessation for more than 24 hours. In contrast with the winter rains, those of the summer most frequently come as thundershowers, and while the precipitation

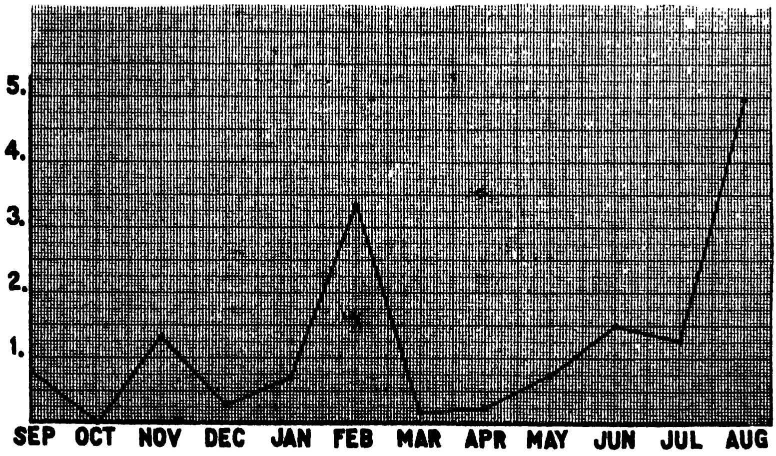

FIG. 2. Rainfall in inches for the months from September 1, 1930, to August 31, 1931.

may be extremely heavy, it is rarely of long duration. Run-off is, of course, great, and penetration correspondingly slight in rains of this type.

The mean depth of precipitation per shower over the area was .35 inches. A comparison of this amount with the average depth recorded by each gauge reveals a considerable variation over the total region. It cannot be said with certainty, however, that there are any very definite trends toward greater or lesser rainfall in successive gauges at about the same elevation, the readings varying from one another in no very definite direction.

In contrast with the mean precipitation of the various stations is the condition found in certain storms, particularly in the summer, that cover only a small area, and have a maximum intensity at the center, tapering off quite rapidly at the edges. In storms of this type the variation between gauges is greatest, and a very distinct gradient is evident from one edge of the observational area to the other. The rain of August 3, 1931, is of this type (fig. 1, *A*), and represents the greatest variation observed in any one storm, as well as the most definite gradient from one end of the area to the other. This storm also indicates to a marked degree the intensity that may be attained in the summer rains. During a 45 minute period about the middle of the afternoon, 1.51 inches fell at the Laboratory buildings, while the gauge in the series under discussion that received the heaviest rain recorded 1.40 inches.

Contrasted with this are storms of the type exemplified in the precipitation of July 13, 1931 (fig. 1, *C*). This was of relatively short duration, lasting only one hour and forty minutes, but not exhibiting a definite increase in any one direction. In this latter respect it resembles the winter rains.

Approaching and ascending the hill, a rather consistent increase is evident, indicating a possible correlation between even this slight increase in altitude and total annual precipitation. It should be noted, however, that this increase is not present in all rains, and readings from a number of years might not bear out the apparent correlation observed in a single year's observation.

Care must be exercised in drawing conclusions from these rather limited data. It is probable that the different stations on the level ground would show an increasing tendency to approach their common mean if continued for several years. This is indicated by the fact that a comparison of the readings of adjacent gauges reveals that even in those cases in which there is a comparatively large mean difference, this is not due to a consistently heavier rainfall in one gauge as compared with another, but rather to large differences in a few of the heaviest rains.

There is no evidence that these local variations have any appreciable effect on vegetation. Any temporary results would be offset by subsequent rains.

SUMMARY

1. The mean annual rainfall in the various gauges was in almost all cases different, and in some cases varied rather widely. It is assumed that the flattening of the individual differences between the various gauges which took place in one year would be still more pronounced if the readings were continued over a number of years.

2. The highest annual means are not due to consistently heavier precipitation at those stations but to great local variations in certain of the heaviest showers.

3. A slight but progressive increase of rainfall with increasing altitude was found up to the highest station at an elevation of 600 ft. above the plain.

4. The winter rains tend to be more uniform in local as well as general distribution than those of the summer, although exceptions occur in both seasons. The summer rains tend to be shorter in duration and more severe than those of the winter type, and since they are often quite local, may show a definite gradient from one end of a small area to the other. Winter rains do not ordinarily exhibit a gradient over so small an area as the one under observation.

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VALUES AND LIMITATIONS OF CLIPPED QUADRATS[1]

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Many investigators have used the clipping method to obtain data representing the effects of varying intensities of harvesting grasses and other herbaceous vegetation. The work of Sarvis ('23), Sampson and Malmsten ('26), and Aldous ('30) on range grasses; Ellett and Carrier ('15), Graber, *et al* ('27), and Stapledon and Milton ('30) on crop and pasture plants; and Harrison ('31) on the maintenance of turf on golf courses; illustrate the breadth of the field in which the method has been used. In range research, the yield and vigor of grasses under varying degrees of use have been the principal data desired to supplement actual grazing experiments. Many tests have shown the effects of various treatments upon the quality of the vegetation and also upon plant succession.

Methods of Clipping

Clipping studies usually are established with a series of meter square or similarly sized quadrats with one or more forage species represented, and clipped uniformly at heights varying from 1 to 4 inches, and at intervals from every week to one cutting at the end of the growing season. The clipped vegetation usually is weighed both green and air dry, and samples are analyzed to determine the quality of the forage produced under the different treatments. The quadrats are mapped once or oftener each year to show the area changes of the plants.

Limitations of Clipped Quadrats

Clipping studies serve as a valuable supplement to grazing experiments but their limitations must be recognized and given proper consideration in the interpretation and application of results. In crop and turf studies, the experimental results should be almost directly applicable in the field, but there are several points of difference between clipping and actual grazing by live stock, which prevent direct and unqualified application of the results in range management.

One of the principal differences between clipping and grazing is the manner in which the forage is removed. In clipping, the vegetation is cut uniformly over the quadrat at a given height, while livestock mainly pull

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and break off the flower stalks and leaves at a convenient height, which varies considerably with different species of forage or with different classes of stock. Whether or not there is a marked difference in plant reaction to injury by cutting or by breaking can be determined only by experiment. If studies are desired to simulate grazing, the solution may be found in harvesting the forage, not by cutting, but by pulling the leaves and stems in a manner as similar as possible to the actual grazing of the particular class of livestock for which the results are desired.

Another difference is that the natural preferences of livestock are not simulated in clipping studies, particularly where more than one species is involved in the same study. When range is conservatively grazed, the utilization by livestock is very patchy, with some small areas a few feet across, of vegetation eaten to within a few inches of the soil surface, and other adjacent small areas hardly touched. Also where there are several forage species on an area, one or more may be taken with relish to within one or two inches above the soil surface, while other species are eaten only sparingly to within 4 to 6 inches of the soil. On yearlong range, two or three species may be eaten only in the summer and autumn, while other species are relished throughout the year. These are features which have not been reflected in clipping studies, but which can be provided for if the purpose of the study is to imitate grazing as closely as possible.

Comparatively small quadrats are required for convenience in mapping and for accomplishing the measurements and clipping within a reasonable length of time. With plots as small as one meter square, there is some question as to the accuracy of results, unless the quadrats are selected very carefully. The error is reduced, of course, by performing the clipping on as many sets of duplicate quadrats as time permits.

The disturbance of both the vegetation and the soil on clipped quadrats is not comparable to that caused by the trampling of livestock on a grazed area. The borders of quadrats clipped most often may be well trampled by the worker, while vegetation on the plots themselves is not trampled at all, a situation which does not occur on grazed range. Furthermore, the effects of trampling by stock on different forage species and soil types can be obtained only on grazed plots. Even though it may be negligible on conservatively grazed range, trampling and its effects on reseeding and plant growth must be considered as a range factor not accounted for in clipping studies.

The accumulation of litter on clipped quadrats differs from that on grazed range. Clipping even once a season allows practically no leaves or flower stalks to drop to the soil surface, while under conservative or even full use of the range, considerable litter is contributed to the soil every year, and even more when the range use is deferred. The loss of litter permits erosion of the top soil away from the root crowns of the grass tufts and reduces the amount of moisture seeping into the soil. Continued erosion affects adversely the yield of the clipped quadrats as was noted by Sampson and Weyl ('18) in studies of forage production on eroded and noneroded soils.

Value of Clipped Quadrats

The principal objections to the clipping method arise from the fact that it does not simulate actual grazing. Nevertheless, clipping studies offer the most direct and accurate method of obtaining, under definite control, results which show the actual yield of range and pasture plants, and the relationship of yield to moisture supply and intensity of stem and foliage removal. The value of the method in range research depends in part upon the purpose for which it is used. If data are desired which unquestionably reflect actual grazing, the method commonly used must be perfected to remove the limitations. Many of these questionable features can and should be eliminated in the future; but for the present, when cost is such an important item, facts of great importance in range and pasture management may be brought to light and put into use, if the true purpose and proper application of the results is understood clearly. Results showing the effects of degree and frequency of clipping and of rainfall on the yield, vigor and nutritive value of plants at different seasons of the year can be used as indications guiding and supplementing actual grazing studies and practice.

Clipping studies, carefully selected and conducted may show many desired relationships, some of which follow:

1. Forage yield each year over a period of years.
2. Variation in yield between species.
3. Relation of yield to soil moisture.
4. Relation of tuft area or plant cover to soil moisture.
5. Relation of both yield and tuft area to frequency and degree of harvesting.
6. Relation of height growth, leaf length, number of flower stalks and tuft area to yield.
7. Relation of nutritive and mineral values of clipped material to soil moisture and to frequency and degree of harvesting.
8. Probable trends in plant succession under different degrees of cutting.

One additional use of clipped quadrats is for the securing of data showing comparative forage production on large range units each year. Especially on winter or yearlong ranges, representative plots could be established, charted, clipped to appropriate height, and the resulting data used as an index of forage production. Under this system, the quadrats selected would be used for only one year with a new set located on representative areas of the range every year, because the reaction of the vegetation to complete harvesting would leave it in a condition unrepresentative of general production the following year.

Application of Results

The most important problem in range and pasture management is the determination of numbers of stock that a given unit will support with sustained profit to the owner and with proper conservation of the resources involved. Assuming that proper class and distribution of livestock on the unit are in effect, the questions of proper numbers and season of use lead directly to the problem of proper forage utilization, which is: just how closely may the important palatable plants be grazed without impairing their growth, vigor, and future productivity. It is upon this important problem that clipping studies can show some very forceful indications. For instance, in 1915, it was thought that *Bouteloua eriopoda* in southern New Mexico could be maintained permanently when used each year to within 1.5 inches of the ground. Clipping studies on the Jornada Experimental Range have indicated however, that complete cutting at two inches above the soil surface is too intense under the rainfall conditions obtaining there. Similar studies with the same species on the Santa Rita Experimental Range, with higher rainfall than the Jornada, have indicated that clipping to two inches above the ground will permit maintenance of the species in many parts of Southern Arizona. Actual grazing practice has shown the truth of these findings. Thus, extremely valuable indications have been obtained as to what constitutes proper grazing of this important species in two different climatic locations. Further indications of adjustments in grazing practice are in view when final analysis of seven years results on the two studies is completed.

The findings of Sampson and Malmsten ('26) in Utah have led to greatly improved grazing practice on the National Forests. Their outstanding results were the determination of proper degree and frequency of grazing throughout the summer, the effects of seasonal harvesting, and the serious effects of too frequent harvesting of the forage, either in the early stages of development or after seed maturity. In addition, their results pointed out desirable tests to make under actual grazing conditions.

Summary

Clipping treatment may be applied to the field almost directly in work with field crops and turf. It fails to simulate grazing by livestock exactly, but in spite of the differences, many of which may be overcome, clipped quadrats when carefully selected and conducted, can be of immense value to actual grazing studies. Results can be obtained at rather low costs to show the comparative maintenance, yield and quality of forage species under known varying intensities of harvesting, with the effects of given amounts and character of rainfall upon production. The method already has aided greatly in the determination of correct utilization of range and pasture forage, a feature which is vital for the proper conservation of the forage and watershed resources. When used with perfected technique and judicious interpretation of results, it should prove to be even more valuable than it has been in the past.

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STUDIES OF CHEMICAL CONTROL OF RELATIVE HUMIDITY IN CLOSED SPACES

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Biological workers have experienced difficulty in determining relative humidity in small cages and similar spaces. It has been a common practice to use chemical solutions to control the humidity in closed containers, but because of the difficulty of measuring the moisture content of the environments the theoretical or reported values produced by the chemical compounds have been accepted as accurate by a number of workers.

STATEMENT OF PROBLEM

This investigation dealt entirely with the use of supersaturated chemical solutions for the control of relative humidity in small closed containers. The questions in mind were: (1) What is a convenient and reasonably accurate method for measuring the relative humidity in small closed containers? (2) Can the reported relative humidity values for supersaturated solutions of various compounds be depended upon as accurate without being measured in each case? (3) Will the relative humidity remain constant over a long period of time? (4) How long can the containers be left open without greatly disturbing the established equilibrium? (5) How long does it require for the equilibrium to be reestablished after it is once lowered?

REVIEW OF LITERATURE

The International Critical Tables (National Research Council, '26) is a common source of reference for the approximate relative humidity that can be maintained with the various compounds. Griffiths ('25) gives an excellent discussion of the determination of humidity in closed spaces by various methods. Gray ('29) described a cog psychrometer as suitable for the measurement of humidity in small spaces. This type of instrument yielded very grave errors in certain environments used in this study. Smith ('31) reported on a study of methods of measurement and the moisture conditions in a number of types of open insect cages, but did not investigate the relative humidity in closed cages.

METHOD OF PROCEDURE

Pint milk bottles were used as containers throughout the experiments. Bottles were selected that permitted good visibility in order that the early formation of the moisture film on the dewpoint apparatus could be detected.

The supersaturated solutions listed in table I were used to obtain the various humidity conditions. Sufficient liquid was used to completely cover the bottom of the containers. All of the chemicals were of "C. P." grade, with the exception of sodium chloride, which was the commercial salt.

The air temperature of the chambers was maintained at a constant level, with a variation of about one degree each way. The air was not kept in motion, thus accounting for the slow response of the thermo-regulator and for some variation of the temperature in different parts of the chamber. Three different temperatures, 22°, 27°, and 32° centigrade, were used.

The relative humidity of the chambers remained fairly constant during the experiment, averaging 36 per cent at 32°, 57 per cent at 27°, and 32 per cent at 32°, with a range of about ten per cent in each environment at various times, when open exposures of the containers were made.

The humidity of the containers was measured with a cog psychrometer modeled after Gray ('29) and a dewpoint apparatus (Marvin, '15; Griffiths, '25). The dewpoint apparatus was modified from that of Marvin and Griffiths by placing a thermometer on the outside of the instrument so that the bulb was about one-sixteenth of an inch from the metal where the dew formed and on a level with the bulb of the thermometer on the inside on the metal thimble. Both thermometers were read at each determination of the relative humidity. The apparatus was placed in the chamber and permitted to attain the temperature of the surroundings before being used. A chamber door, made from heavy cardboard, with two arm-holes and a glass window was used so that determinations could be made without disturbing the temperature of the environment.

When using either instrument the cork was removed from the bottle and the instrument inserted immediately, permitting the bottle to be open for a second or two, or less, during the operation. Determinations with the dewpoint apparatus were made also by placing the instrument, ready for use, in the containers and allowing a temperature and moisture equilibrium to be established before the determinations were made. No significant differences resulted by this method from that where the cork was removed and the apparatus quickly inserted. Usually the difference was two per cent or less. Following this a number of readings were taken after the containers had been left open for various intervals. Several hours were permitted to elapse between measurements of the humidity in any given container.

EXPERIMENTAL RESULTS

When the solutions were made up an equilibrium was established in a short while, in some cases requiring only a few minutes. If the chemicals and water had reached the chamber temperature before being mixed, an equilibrium was established much more quickly than when the materials were at a lower temperature. In a few instances the heat of reaction of the chemicals in water rapidly established a high moisture environment, which was soon reduced. If the proper mixture was used the containers were ready for use in less than an hour.

Cog Psychrometer. The type of cog psychrometer recommended for small spaces by Gray ('29) was tried at first. Apparently accurate results were obtained in the high moisture environments, but very grave errors, as much as 30 per cent, resulted in the low moisture conditions, when checked biologically with insect eggs and by the dewpoint method (table I). It was difficult to place the wet and dry bulbs of the thermometers far enough apart in the type of container used to avoid cooling of the dry bulb. However, this was not a factor in the above error. The error could be lowered slightly by reducing the amount of water placed on the cloth, but not sufficient to make the use of the cog psychrometer practical with moisture environments below about 70 per cent.

Dewpoint Method. When it was demonstrated that the cog psychrometer was not suitable, measurements by the dewpoint method were undertaken. Griffiths ('25) states, "Of the three physical methods of hygrometry, the dewpoint apparatus stands out conspicuously as being the one instrument which has a sound theoretical foundation and, further, it has the practical advantage that it is as easy to manipulate at low temperatures, as at room temperatures." The writer has found the dewpoint method efficient and as convenient for small spaces as any method tried. However, it takes some practice to detect the early formation of the moisture film. In the early stages of this investigation considerable errors in observing the moisture film were made. The data in table I show that the dewpoint determinations approach the reported values very closely in the dry environments. This result was checked biologically also, by using insect eggs that should have hatched if the humidity was as high as indicated by the cog psychrometer measurements.

TABLE I. *A comparison of relative humidity in various closed environments at 22°, as determined with the cog psychrometer and dewpoint apparatus*

Solutions	Relative humidity		
	Cog psychrometer	Dewpoint apparatus	Reported values
H_2O	96	96	100
K_2SO_4	94	92	95
$ZnSO_4$	89	83	90
KBr	82	79	84
NaCl	76	75	76
$NaNO_2$	69	64	65
$NaHSO_4$	81	63	51
KNO_2	81	63	42
$CaCl_2$	60	32	32
$KC_2H_3O_2$	51	25	20
LiCl	44	12	14

An examination of the data in the table shows that the reported values cannot be accepted as accurate, even when fresh " C. P." chemicals are used. This is shown by the absence of data between 32 and 63 per cent of relative humidity in the second column. Two salts, sodium bisulphate and potassium nitrite, are reported to fall within this range at this temperature. Apparently potassium nitrite is not a reliable salt to use, as unexplained variations or errors in measurement were recorded in that container. This was especially true in the 27° and 32° environments. No consistent variation from the average of these or any of the other salts was observed.

No appreciable changes in the relative humidity that was maintained by the various solutions occurred during the course of the experiments, an interval of six months.

The results at the three temperatures, 22°, 27°, and 32° centigrade, are given in tables II, III, and IV. The humidity, when equilibrium was established, is given in the first column of the tables. Open exposures of the containers to the chamber conditions were continued for two-minute, five-minute, fifteen-minute, and one-hour intervals. Humidity determinations were made at the end of the respective periods. Each result in the tables was established from the average of several determinations.

An examination of the data in these tables shows that the moisture equilibrium was changed very rapidly during the first two minutes that the containers were open. The change became very gradual after about five minutes' exposure. In biological experimental work, where chemicals are used to control the humidity, it probably would not be necessary to have the containers open more than a few seconds at a time, so that the change should be much less than during a continuous exposure of two minutes. However, the change might be much greater if the containers are exposed to a temperature different from that of the chamber temperature. The chamber humidity in the 27° environment (table III) was about 20 per cent greater than in the 22° and 32° conditions. Nevertheless a very rapid change occurred in the high humidity containers.

If an equilibrium is re-established quickly after the containers are closed, very little error would be introduced. This was tested by exposing the open containers to the chamber conditions for two minutes, then closing them for fifteen minutes, after which the relative humidity was measured (tables II, III, IV). An equilibrium was quckly reestablished in the 32° chamber. The water and potassium sulphate containers were five per cent below equilibrium when tested. In the 27° chamber, two containers had not reached an equilibrium in fifteen minutes, water being four per cent minus and lithium chloride three per cent plus. The average humidity in this chamber was 56 per cent. Apparently a little more time was necessary for reestablishment of equilibrium in the 22° chamber as the water and potassium sulphate containers at the end of fifteen minutes had humidities eleven per cent and nine per cent minus respectively.

TABLE II. *The relative humidity maintained by various supersaturated solutions in containers under open and closed conditions. The chamber temperature was 22° centigrade and the average relative humidity 36 per cent with a spread of about 10 per cent.*

Solutions	Closed container	Open exposure				Open 2', closed 15'
		2'	5'	15'	60'	
H_2O	96	86	81	80	78	85
K_2SO_4	92	85	79	76	72	83
$ZnSO_4$	83	77	74	73	71	84
KBr	79	73	71	69	67	78
NaCl	75	73	73	71	68	73
$NaNO_2$	64	66	62	64	60	65
$NaHSO_4$	63	64	61	60	62	65
KNO_2	63	64	63	61	56	61
$CaCl_2$	32	32	30	33	29	33
$KC_2H_3O_2$	25	23	24	26	22	23
LiCl	12	12	14	13	14	14

TABLE III. *The relative humidity maintained by various supersaturated solutions in containers under open and closed conditions. The chamber temperature was 27° centigrade and the average humidity 56 per cent with a spread of about 10 per cent.*

Solutions	Closed container	Open exposure				Open 2', closed 15'
		2'	5'	15'	60'	
H_2O	95	90	87	85	82	91
K_2SO_4	92	84	84	82	82	91
$ZnSO_4$	81	78	78	74	71	80
KBr	77	78	78	76	71	76
NaCl	77	70	69	70	66	75
$NaNO_2$	60	61	59	58	60	61
$NaHSO_4$	68	64	63	61	60	68
KNO_2	67	66	62	59	56	65
$CaCl_2$	28	30	31	28	31	30
$KC_2H_3O_2$	29	28	28	25	26	28
LiCl	12	16	16	12	20	15

TABLE IV. *The relative humidity maintained by various supersaturated solutions in containers under open and closed conditions. The chamber temperature was 32° centigrade and the average relative humidity 32 per cent, with a spread of about 10 per cent.*

Solutions	Closed containers	Open exposure				Open 2', closed 15'
		2'	5'	15'	60'	
H_2O	97	78	81	78	74	92
K_2SO_4	95	81	84	76	75	90
$ZnSO_4$	76	67	68	64	67	76
KBr	80	75	66	65	64	77
NaCl	71	60	60	58	63	72
$NaNO_2$	58	55	54	53	52	60
$NaHSO_4$	64	62	62	60	54	59
KNO_2	63	53	52	59	57	61
$CaCl_2$	26	23	25	24	24	25
$KC_2H_3O_2$	21	22	21	19	22	23
LiCl	13	12	13	10	14	12

CONCLUSIONS

The dewpoint method is a convenient and efficient method of measuring relative humidity in small closed containers. The cog psychrometer is not a suitable instrument for such purposes.

The reported relative humidity that can be obtained with various super-saturated solutions cannot be accepted as accurate without being checked.

The humidities obtained with chemical compounds did not change during a period of six months under the conditions tested.

The established moisture equilibrium was changed very rapidly in the containers when they were exposed to external humidities greatly different from the internal humidity.

The moisture equilibrium was quickly reestablished after the containers were closed at 22°, 27°, and 32° centigrade.

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FURTHER STUDIES OF THE PHYSICAL ECOLOGY OF THE ALFALFA WEEVIL, *HYPERA POSTICA* (GYLLENHAL)[1,2]

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This is the third of a series of papers on the physical ecology of the alfalfa weevil. The first (Sweetman, '*29*) dealt with the physical conditions in an alfalfa field and detailed studies of the habits of the pest. The second report (Sweetman, '32) comprised a study of the effects of temperature and moisture on development of the insect under field conditions. This paper considers these factors as they affect the weevil in controlled laboratory environments.

The problem was undertaken in an attempt to determine the probability of the alfalfa weevil becoming established in the Mississippi Valley States. It is believed that this can be accomplished by determining the effects of the climatic factors which limit the abundance and distribution of the pest. This paper is the final report of the senior author, but much still remains to be done before the problem is solved. It is hoped that his successor will be able to carry the project to completion.

Review of Literature

A few workers have made estimates of the effects of temperature and moisture on the alfalfa weevil. The opinion that warm, dry weather in the spring is favorable to the insect's development is common (Titus, '13; Wakeland, '20; Snow, '25; Cook, '25). However, Newton ('25) states that injury was greatest during cool, wet springs. The difficulty of isolating the factor or factors that control development in the field probably accounts for the difference in interpretation cited above: Reeves ('27*a*) seems to have separated the influences of temperature and moisture more completely than other workers and he believes that temperature is very important but that moisture is a minor factor. Earlier, Reeves ('17) concluded that no evidence was available that would preclude the dispersal of the weevil in the East and later ('27*b*) predicted that the insect would become established in all alfalfa growing regions. In 1925, Reeves stated that the weevil lives in all climates.

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[1] Published by permission of the Wyoming Agricultural Experiment Station.

[2] Cost partially defrayed from funds other than those of the Ecological Society.

METHOD OF PROCEDURE

The effects of temperature and moisture on the alfalfa weevil were studied in controlled artificial environments. This makes it possible to determine the responses of the insect during its various stages of development to the individual factors. While field studies are very important to determine what actually takes place under natural conditions and for checking the controlled environments, the interactions of the various factors on the insects cannot be established from such studies alone. The laboratory experiments were conducted in controlled temperature and humidity chambers. The air was forced over large pans, containing concentrated salt solutions, in the bottoms of the experimental chambers with electric fans. The direction of the air currents was over the pans and up through the experimental cages that contained the insects. The humidity at the level of the cages was measured with recording hair hygrometers, which were standardized frequently. The technique of handling the various stages was similar to that described for field conditions (Sweetman, '32). Food was supplied from outdoor or greenhouse grown plants. Adults and immature stages were exposed to both constant and varied temperatures and moisture environments. The data to be presented are not complete enough for the drawing of final conclusions regarding the effects of temperature and moisture on the alfalfa weevil.

EXPERIMENTAL RESULTS

Adult Stage. The effects of constant environments with temperatures ranging from 27° to 42° C. at intervals of 5° are shown in table I. High,

TABLE I. *The effects of constant temperature with constant relative humidity on the adults of the alfalfa weevil*

Relative humidity	Number of beetles		Number of beetles died		Number of eggs						
Per cent	♂	♀	♂	♀	1st week	2d week	3d week	4th week	5th week	6th week	Total
					Temperature 27° C.						
32	3	5	1	3	110	43	2	0	0	0	155
60	3	5	1	1	39	0	29	198	194	56	516
93	3	5	0	0	157	124	111	165	131	20	708
					Temperature 32° C.						
32	3	5	2	0	0	0	0	0	0	0	0
67	3	5	0	0	5	1	0	0	0	0	6
88	3	5	1	1	4	8	0	0	0	0	12
					Temperature 37° C.						
32	3	5	3	4	5	0	0	0	0	0	5
56	3	5	2	3	0	0	0	0	0	0	0
90	3	5	3	5	63	0	0	0	0	0	63
					Temperature 42° C.						
32	3	5	3	5	0	0	0	—	—	—	.0
53	3	5	3	5	0	0	0	—	—	—	0
90	3	5	3	5	0	—	—	—	—	—	0

medium, and low moisture conditions were used. Data were secured at 22° also, but are not included in the table, since the air was not kept in motion, which makes the humidity records unreliable. The relationships with moisture showed the same tendencies as the results at 27°. The beetles exposed to 27° and 32° had the same previous history and were placed in the environments simultaneously so the results are directly comparable. The same is true of the beetles maintained at the higher temperatures.

When the temperature was 27° the number of eggs laid was in direct proportion to the humidity of the environment, showing that a high humidity of 93 per cent was very favorable for oviposition and longevity while a humidity of 32 per cent was unsuitable for both phenomena. The beetles were laying when first exposed to the controlled environments. Apparently most of the egg laying in the 32 per cent condition was due to the stimulus of the surroundings preceding the time of the experiment, as most of the eggs were deposited during the first week of exposure. None of the females died until the fourth week. A medium humidity of 60 per cent was stimulating to egg production. Varied conditions were obtained by transferring the cages from one environment to another at definite intervals (table II).

TABLE II. *The effects of constant temperature with varied relative humidity on the adults of the alfalfa weevil*

Relative humidity Per cent Daily exposure of		Number of beetles		Number of beetles died		Number of eggs						
8 hrs.	16 hrs.	♂	♀	♂	♀	1st week	2d week	3d week	4th week	5th week	6th week	Total
						Temperature 27° C.						
32	60	3	5	1	0	166	16	0	0	0	0	182
32	93	3	5	1	2	0	0	0	0	0	0	0
60	32	3	5	1	0	71	97	23	3	23	6	223
60	93	3	5	1	1	0	0	0	12	0	0	12
93	32	3	5	0	1	0	0	0	0	0	0	0
93	60	3	5	1	0	0	0	0	0	0	0	0
						Temperature 32° C.						
32	67	3	5	0	2	17	44	0	0	0	0	61
32	88	3	5	0	1	7	0	0	0	0	0	7
67	32	3	5	0	3	30	9	0	0	0	0	39
67	88	3	5	1	3	0	0	0	0	0	0	0
88	32	3	5	2	0	0	0	0	0	0	0	0
88	67	3	5	0	0	10	3	0	0	0	0	13

Apparently the only females laying at the beginning of the experiment were in the drier environments. The deposition of eggs in these conditions w soon reduced, as occurred under constant conditions with low humidity. One beetle was stimulated to lay a few eggs in the wettest environment.

A temperature of 32° C. was much less favorable than 27° as laying beetles discontinued oviposition after the second week (table I). The females in the low moisture environment were not laying so the effects of humidity are not determinable. Apparently this temperature is unfavorable since medium and high humidities were favorable for oviposition at 27°. No difference in longevity between high and low moisture conditions at this temperature is shown. When the results from varied moisture surroundings are studied the unfavorableness of the high temperature is apparently re-emphasized since no eggs were laid after the second week (table II). The drier environments at this temperature appear to be superior to the moist conditions for egg production, but oviposition was stopped during the second week in all humidities.

The effects of alternation of temperatures of 27° and 32° C. on the beetles are shown in table III. None of the females was laying in the low humidity conditions when the experiment was started and none was stimulated to reproduce. The beetles were laying in the medium and high humidity environments with 16 hours daily exposure to 27° and continued for several weeks, although the total egg production is far below that found under constant environments at 27°, which indicates a detrimental effect of the 32° temperatures. The death rate was much greater under the high than under the medium and low humidity environments at these alternated temperatures.

TABLE III. *The effects of varied temperature with constant relative humidity on the adults of the alfalfa weevil*

Temperature ° C. Daily exposure of		Relative humidity	Number of beetles		Number of beetles died		Number of eggs						
8 hrs.	16 hrs.	Per cent	♂	♀	♂	♀	1st week	2d week	3d week	4th week	5th week	6th week	Total
Relative Humidity—Low													
27	32	32	3	5	2	2	0	0	0	0	0	0	0
32	27	32	3	5	1	0	0	0	0	0	0	0	0
Relative Humidity—Medium													
27	32	60–67	3	5	1	0	0	0	0	0	0	0	0
32	27	67–60	3	5	0	3	71	0	25	123	2	0	221
Relative Humidity—High													
27	32	93–88	3	5	3	2	0	0	0	0	0	0	0
32	27	88–93	3	5	2	2	88	22	72	167	0	0	349

High temperatures of 37° and 42° C. proved to be very detrimental to egg production and longevity in all environments (table I). The data from the varied conditions at these temperatures are not included as they are substantially the same as shown in table I. Laying beetles at 37° ceased oviposition after the first few days. No oviposition occurred at 42°. Longevity was much reduced as compared to that in lower temperatures, all of the beetles dying during the first three weeks exposure. The length of life was least in the high moisture surroundings.

The combined effects of temperature and moisture are shown graphically in figure 1. The data in table I and from the varied environments are included. The results were used only from the cages where eggs were laid except at 42° C. Apparently the lowest temperature, 27°, is the only one that is near the favorable region for egg production. Temperatures above 30° appear to be unfavorable for oviposition. There is some indication that the low humidities are less favorable for reproduction than high humidities at 27°.

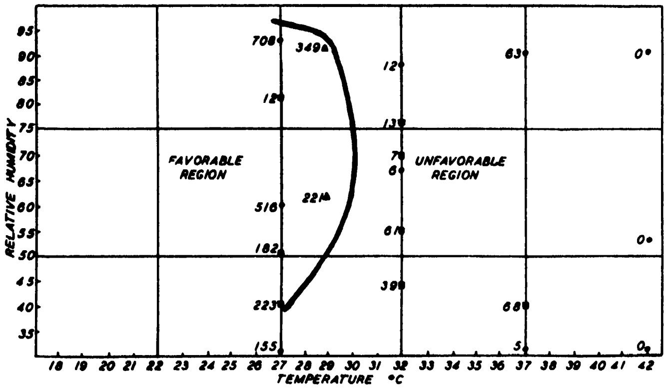

Fig. 1. The combined effects of temperature and relative humidity on oviposition of the alfalfa weevil. The number of eggs laid in constant and varied environments. ● — constant temperature and moisture; ▲ — varied temperature and constant moisture; ■ — constant temperature and varied moisture.

Egg Stage. The eggs were exposed to constant temperature and moisture environments ranging from 17° to 42° C. The results of the constant environments are shown in table IV. Apparently a temperature of 17° with 50 per cent humidity is near the minimum temperature or humidity, or both, at which the eggs will hatch, as larvae emerged from 17 per cent only, although 26 per cent of well-developed embryos failed to hatch. This latter condition probably was produced by the low humidity. Two series of results from experiments at 22° are shown. The second was conducted before fans were installed in the cabinets and the humidity probably was lower than indicated in the table, but the results in both series show the same tendencies. The temperature was very favorable for hatching of the eggs with high humidity and rather unfavorable with 40 and 60 per cent humidities. Most of the developed embryos hatched in the moist conditions while 36 per cent failed to hatch in the 40 per cent condition. The length of the incubation periods was least in the high humidity environments. Three series of data were obtained from experiments at 27°. The results are in agreement with those taken in 22° conditions in every way except the length of the incuba-

TABLE IV. *The effects of constant temperature with constant relative humidity on the incubation of the eggs of the alfalfa weevil*

Relative humidity	Total number of eggs	Total number hatched	Per cent hatched	Days to hatch	Per cent of unhatched embryos
Per cent					
		Temperature 17° C.			
50	46	8	17.4	19.8	26.1
		Temperature 22° C.			
40	50	10	20.0	12.1	36.0
86	45	32	71.1	9.2	8.9
40	73	0	0.0	—	—
60	100	22	22.0	11.0	—
90	126	97	77.0	9.4	—
		Temperature 27° C.			
80	46	25	54.3	6.8	6.5
32	95	2	2.1	8.0	53.7
60	90	60	66.7	6.8	8.8
93	88	68	77.3	6.1	2.3
32	30	1	3.3	9.0	—
60	102	51	50.0	7.4	—
72	27	7	26.0	7.0	—
79	55	31	56.0	7.3	—
93	35	27	77.0	6.9	—
		Temperature 32° C.			
32	47	0	0.0	—	10.6
92	41	19	46.3	5.8	29.2
32	82	2	2.4	7.5	26.8
67	97	36	37.1	6.5	30.9
88	88	55	62.5	5.5	13.6
		Temperature 37° C.			
40	48	0	0.0	—	—
75	82	0	0.0	—	—
90	81	0	0.0	—	—
32	14	0	0.0	—	0.0
56	11	0	0.0	—	0.0
90	12	1	8.3	4.0	33.3
		Temperature 42° C.			
32	12	0	0.0	—	0.0
53	10	0	0.0	—	0.0
90	11	0	0.0	—	0.0

tion period, which is reduced to about one week. Only a low percentage of the eggs hatched in the low humidity, but 54 per cent of the eggs contained well-developed embryos that failed to emerge. The data from two series of experiments are shown for a temperature of 32°. The injuriousness of the high temperature is apparent. The high humidity is still superior to low humidities at this temperature, but a greater percentage of the well-developed embryos failed to hatch. A low percentage of the embryos developed in the dry environments. The length of the incubation period is reduced, especially in the higher humidities. Temperatures of 37° and 42° are too high for good embryonic development regardless of humidity conditions. A few embryos developed and one egg hatched at 37° with 90 per cent humidity, but the embryos failed to develop at 42°. A few eggs from the same series were used as a check on the eggs exposed to the high temperatures. They were placed in an environment of 27° with high humidity. Excellent hatches resulted, showing that the failure to hatch in 37° and 42° conditions was due to the high temperature.

Constant temperatures with varied humidities were used with environments ranging from 22° to 42° C. (table V). Good hatches resulted in 22° conditions even when the eggs were exposed to a humidity of 40 per cent

TABLE V. *The effects of constant temperature with varied relative humidity on the incubation of the eggs of the alfalfa weevil*

Relative humidity—Per cent						
Daily exposure of		Total number of eggs	Total number hatched	Per cent hatched	Days to hatch	Per cent of unhatched embryos
8 hrs.	16 hrs.					
Temperature 22° C.						
40	86	48	31	64.6	9.6	4.2
86	40	50	35	70.0	10.3	6.0
Temperature 27° C.						
32	60	77	32	41.6	8.4	22.1
32	93	76	45	59.2	6.6	13.2
60	32	109	35	32.1	8.9	42.2
60	93	65	44	67.7	6.8	12.3
93	32	69	39	56.5	7.4	24.6
93	60	88	69	78.4	6.7	5.7
Temperature 32° C.						
32	92	39	9	23.1	5.8	20.5
92	32	39	0	0.0	—	2.5
32	67	80	16	20.0	7.0	50.0
32	88	93	37	39.8	5.4	27.9
67	32	74	5	6.8	5.9	48.6
67	88	61	37	60.7	5.6	16.4
88	32	62	10	16.1	5.7	53.2
88	67	80	34	42.5	6.3	25.0

for 16 hours daily. Nearly all of the developed embryos hatched. Apparently a high humidity of 86 per cent for eight hours at 22° was sufficient to overcome the disadvantage of low humidity that was shown under constant surroundings. Data from varied moisture conditions at 27° agree with the results secured under constant environments at this temperature. High humidities produced the best hatches and low humidities the poorest hatches. The length of the incubation period was unchanged from that of the constant environments. The effects of moisture variations at 32° are in close agreement with constant humidities at this temperature. High humidities still gave the best results, but the percentage of well-developed embryos that failed to hatch is greatly increased over that of the 27° environments. Alternated moisture conditions at 37° and 42° proved unsuitable for incubation of the eggs. The data from these conditions are not shown in the table since very little embryonic development occurred, which gave results similar to that of the constant environments. A few embryos developed in the higher humidities at 37°, but these failed to hatch.

The effects of varied temperature environments with approximately constant humidities are shown in table VI. The temperature ranged from 22° to 42° C. Since none of the eggs hatched and very little embryonic development occurred in the 37° and 42° conditions, the results with these temperatures are not included in the table. Combinations of 22° and 32°, 27° and 32°, and 37° and 42° were made in the low humidity range. The detrimental effects of both temperature and moisture combined reduced the hatching to practically zero. The two instances where the temperatures were 22° and 27° for 16 hours produced a few larvae, but when the temperature was above 27° for sixteen hours all of the embryos were killed. Four combinations of varied temperature were used with the medium humidities. Alternations of eggs between 17° and 22° gave results intermediate between the respective constant temperatures. Eggs in the 32° environments were alternated with both 17° and 27°. Exposure to the lower temperatures for sixteen hours gave better hatches than the reverse combination, thus showing a partial offsetting of the effects of the higher temperature. Better hatches resulted with the 27° alternation than the 17° one indicating that 27° was superior to 17° for incubation of the eggs. The 27° combination with 32° also produced better hatches than 32° alone (table IV), again showing that 32° is too high a temperature for best results. Varied temperatures with high humidities ranged from 22° to 42°. These humidities were shown to be decidedly favorable for good hatches with the constant and varied moisture experiments (tables IV, V). Fairly good hatches resulted in all combinations of temperature below 37° indicating that the humidity was a very important factor in reducing the hatch in the medium and low humidity series.

The incubation records in tables IV, V, and VI are shown graphically in figure 2. It is impossible to show the exact effects of temperatures below 22° C. with the data available. The favorable region appears to be confined

TABLE VI. *The effects of varied temperature with approximately constant relative humidity on the incubation of the eggs of the alfalfa weevil*

Temperature ° C.		Relative humidity Per cent							
Daily exposure of		Daily exposure of			Total number of eggs	Total number hatched	Per cent hatched	Days to hatch	Per cent of unhatched embryos
8 hrs.	16 hrs.	8 hrs.	16 hrs.	24 hrs.					
Relative Humidity—Low									
22	32	40	32		43	0	0.0	—	23.2
32	22	32	40		41	4	9.8	9.8	41.5
27	32			32	67	0	0.0	—	25.4
32	27			32	68	2	2.9	7.7	65.3
Relative Humidity—Medium									
17	22	50	40		49	11	22.4	14.2	28.6
22	17	40	50		42	12	28.6	12.9	11.9
17	32	50	32		42	4	9.5	9.3	19.0
32	17	32	50		35	6	17.1	12.0	34.3
27	32	60	67		84	33	39.3	7.3	28.6
32	27	67	60		77	47	61.0	7.6	4.3
Relative Humidity—High									
22	32	86	92		45	24	53.3	6.4	6.6
32	22	92	86		36	22	61.1	7.3	5.5
22	27	86	80		43	20	46.5	7.0	0.0
27	22	80	86		40	20	50.0	8.5	2.5
27	32	80	92		45	21	46.6	6.0	13.3
32	27	92	80		40	26	65.0	5.9	5.0
27	32	93	88		78	49	62.8	5.6	15.4
32	27	88	93		80	49	61.3	6.3	7.5

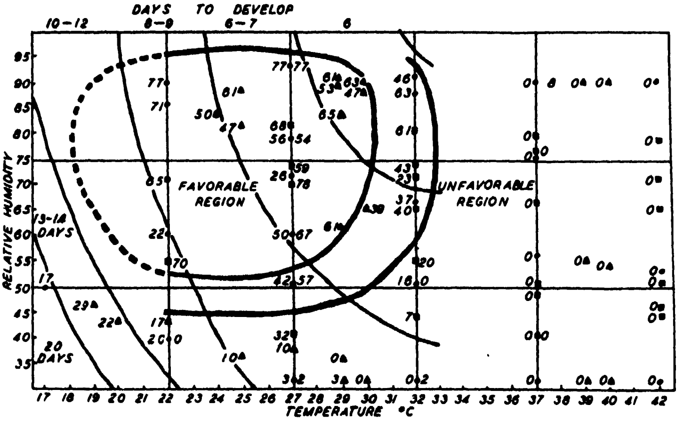

FIG. 2. The combined effects of temperature and relative humidity on the eggs of the alfalfa weevil. The percentage of eggs hatching and rate of development of eggs. ● — constant temperature and moisture; ▲ — varied temperature and constant moisture; ■ — constant temperature and varied moisture.

to temperatures of about 20° to 30° and humidities of 55 to 95 per cent. Since the natural position of the eggs is inside the stems of the plants it is evident that low humidity ordinarily would not be injurious to the eggs as long as the plants are not suffering from lack of water. Temperatures above 32° and humidities below 50 per cent at all temperatures used are very unfavorable for hatching of the eggs.

Sanderson and Peairs ('13) have shown that the theoretical minimum effective temperature for development can be determined by plotting the reciprocal of the hyperbolic developmental curve. The true minimum effective temperature is slightly below this point. The lengths of the incubation periods in table IV are plotted in figure 3 to determine the theoretical minimum effective temperature for incubation of the eggs. The developmental curves (*A*) in high, medium, and low humidity and their reciprocals (*B*) are shown. Apparently the minimum effective temperature for incubation of the eggs is near 10° C. for all humidities from 32 to 93 per cent.

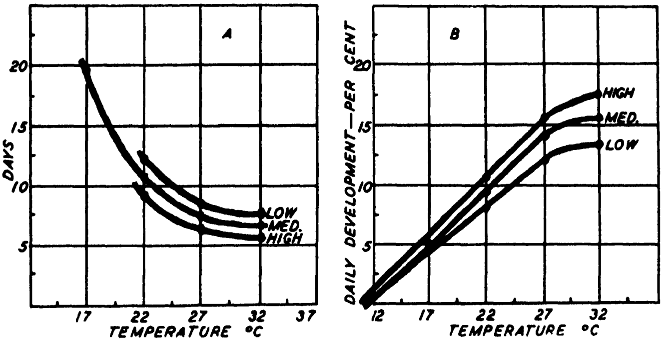

FIG. 3. The growth curves for embryonic development of the alfalfa weevil when exposed to high, medium, and low relative humidity.

Larval Stage. Larvae were exposed to constant environments ranging from 17° to 42° C. (table VII). The difficulties of controlling or measuring humidity within a few millimeters of leaf surfaces was recognized. The maintenance of continuous air currents through the cages tended to facilitate rapid equalization of the transpiration moisture with the surrounding environment. A temperature of 17° with 50 per cent humidity was favorable for maturation of the larvae but development was very slow. The experiment was closed before the larvae transformed to adults, but 34 days were required to reach the pupal stage. Two series of results from experiments at 22° are given. Growth at 22° was greatly accelerated over that at 17° as complete development took place in less time than was necessary for the feeding stage at 17°. The time necessary in high humidities was reduced over that in low humidities. Apparently humidities from 40 to 90 per cent at 22° are favorable to larval development. Three series of results are listed from the 27° environments. Development is accelerated about 20 per cent over

TABLE VII. *The effects of constant temperature with constant relative humidity on the larvae of the alfalfa weevil*

Relative humidity — Per cent	Total number of larvae	Number of larvae died	Number of days feeding	Number of days as prepupae	Number of days as pupae	Number of days to emerge	Total number of days	Per cent reared — Prepupae	Pupae	Adults
				Temperature 17° C.						
50	5	0	28.6	5.2[1]	—	—	—	100	100	(100)
				Temperature 22° C.						
40	9	0	16.7	3.0	6.6	1.6	27.9	100	100	100
86	8	0	15.3	2.6	4.9	3.0	25.8	100	100	100
40	3	1	15.0	2.0[1]	—	—	—	66	66	(66)
60	9	1	16.5	2.5[1]	—	—	—	89	89	(89)
90	3	0	12.7	2.0	5.5	1.5	21.7	100	100	100
				Temperature 27° C.						
80	14	3	9.5	1.7	3.8	1.0	16.0	79	79	79
60	3	0	12.0	1.7	4.0	1.0	18.7	100	100	100
79	3	0	10.8	1.7	4.5	1.0	17.1	100	100	100
32	8	2	11.3	1.5	4.0	1.5	18.3	75	75	75
60	4	0	9.5	1.2	4.8	2.0	17.5	100	100	100
93	10	5	10.6	1.6	4.2	0.9	16.3	50	50	50
				Temperature 32° C.						
32	9	0	7.3	1.1	2.7	0.8	11.9	100	100	100
92	10	1	7.5	1.3	2.9	0.7	12.4	90	90	90
32	8	2	9.5	1.4	3.8	0.7	15.4	75	63	63
67	5	1	8.2	1.5	2.5	1.5	13.7	80	80	80
88	5	0	7.8	1.0	3.0	1.0	12.8	100	100	100
				Temperature 37° C.						
40	17	16	12.0	1.5	4.5	—	—	6	6	0
75	17	16	10.7	1.5	—	—	—	6	6	0
90	18	18	—	—	—	—	—	0	0	0
32	6	5	13.0	—	—	—	—	17	0	0
56	6	5	8.0	2.0	—	—	—	17	17	0
90	6	6	—	—	—	—	—	0	0	0
				Temperature 42° C.						
32	6	6	—	—	—	—	—	0	0	0
53	6	6	—	—	—	—	—	0	0	0
90	6	6	—	—	—	—	—	0	0	0

[1] Experiment closed before development was completed.

that at 22°. Again the shortest developmental time occurred in the high humidities. The death rate in the 27° environments is increased over that at lower temperatures. Two series of results are shown from the 32° conditions. Again the rate of development is accelerated, being about 20 per cent greater than at 27°. The results in the different humidities at 32° are more uniform than in the lower temperatures. Two series of results from experiments at 37° are given. This temperature was too high for good larval development. The larvae died during the feeding period in 90 per cent humidity, but a few were able to reach the prepupal stage in 56 and 75 per cent humidities. One larva pupated in 40 per cent humidity but died in transforming to the adult, while none of the larvae reached the pupal stage in 32 per cent humidity. All of the larvae were destroyed in a few days in the 42° environments.

Environments with constant temperature and varied humidity were used with temperatures ranging from 22° to 42° C. The data are not presented in a table since they are very similar to the results given in table VII. They are included in figure 4. Varied moisture at 22° proved favorable for a high percentage of maturation and apparently an acceleration in development over constant humidities occurred. Growth of the larvae was most rapid in the highest mean humidity. Varied moisture environments at 27° gave results that are in close agreement with those obtained under constant conditions at this temperature. The time necessary for development was rather uniform, but some of the larvae died in all of the environments. The percentage of deaths was much greater than in the 22° constant or alternated conditions. The results at 32° are in complete accord with those found under constant moisture conditions at this temperature. The percentage of deaths was rather high. Varied moisture at 37° did not permit the larvae to reach the pupal or adult stages and only a few reached the prepupal stage. All of the larvae died in a few days in the varied humidities at 42°.

A number of larvae were exposed to varied temperatures with approximately constant humidities. The data are not presented in a table since they are very similar to the results given in table VII. They are included in figure 4. The influences on the larvae when the humidity was low were determined for temperatures ranging from 22° to 42° C. Combinations of 22° and 27° with 32° were very favorable for larval development. The rate of development was proportional to the temperature. The death rate was similar to that found in 22° constant environments, but was much lower than in 27° and 32° constant environments, indicating that varied temperature conditions are more favorable than constant surroundings. The time necessary for development was less than in the constant conditions indicating that the insect's metabolism was accelerated. The larvae died within a few days in the 37° and 42° combinations of temperature. Varied temperatures ranging from 17° to 42° were used with medium humidities. Alternations of 17° and 22° were favorable to larval development although growth was slow. When 32° was alternated with 17° the larvae developed well with only a few deaths occurring. The combinations of 27° and 32° were not as favorable for larval growth, especially when exposed to 32° for sixteen hours. An acceleration of growth was shown, with one exception, over constant environments with medium humidity. The larvae died in a few days in the 37° and 42° conditions. Varied temperatures ranging from 22° to 42° were used with high humidity. Alternations of 22° with 27° and 32° were favorable to larval development in most cases, but when 27° and 32° were alternated the death rate was increased. A stimulating effect of varied temperatures is indicated. The larvae died in a few days in the 37° and 42° conditions.

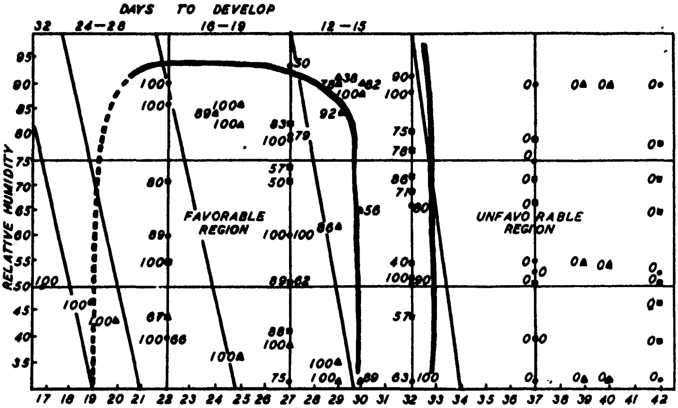

FIG. 4. The combined effects of temperature and relative humidity on the larvae of the alfalfa weevil. The percentages of larvae reaching maturity and rate of development of larvae. ● — constant temperature and moisture; ▲ — varied temperature and constant moisture; ■ — constant temperature and varied moisture.

The effects of various combinations of temperature and humidity on the larvae are shown graphically in figure 4. The figure was made up from the percentages of larvae that developed to maturity in table VII and in the varied environments. The developmental time in the varied surroundings was essentially the same as given in table VII for the constant environments. The favorable region for larval development appears to range from about 20° to 30° C. with humidities from 95 per cent to at least as low as 32 per cent. The intermediate region extends to a temperature of about 34° and humidities at least as low as 30 per cent. The lower temperature range is not determinable from this figure. The region would be defined in the low temperature area by the length of the developmental period as well as the percentage of larvae reaching maturity. Apparently the larvae will not suffer greatly from low humidity as long as the plants remain succulent. Because of this the larvae may be limited largely to irrigated fields in most of the arid west where the pest is found at present. Temperatures above about 34° prevented transformation to the adult stage, while temperatures above 27° to 28° reduced the number reaching maturity.

The total temperature range for development of the larvae has not been established experimentally but the lower limit may be determined mathematically (Sanderson and Peairs, '13). The lengths of the feeding periods under constant temperatures with low, medium, and high humidities are shown in figure 5. The developmental curves are shown in "A" and their reciprocals in "B." The minimum effective temperature for the feeding stage is about 10° C. The influence of humidity near the minimum effective temperature is not so great as at higher temperatures.

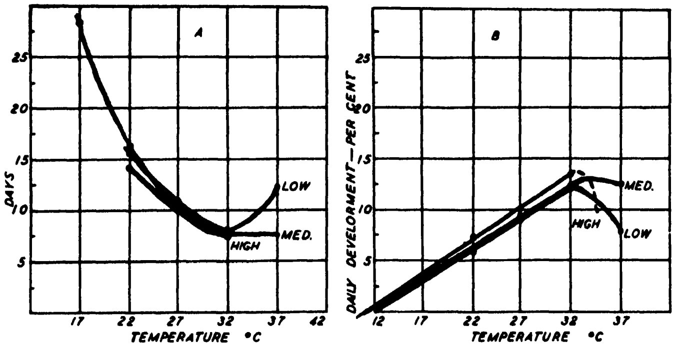

FIG. 5. The growth curves for larval development of the alfalfa weevil when exposed to high, medium, and low relative humidity.

CONCLUSIONS

The favorable region for oviposition of the adults apparently was below a temperature of 28° C. with relative humidities between 50 and 95 per cent. Temperatures of 30° to 37° were very injurious, especially when the relative humidity was high, while higher temperatures killed the adults in a few days. Relative humidities below 40 per cent, at least with temperatures of 27° or higher, were very destructive to the adults.

The favorable region for the hatching of the eggs was between temperatures of about 20° to 30° C. with relative humidities of 55 to 95 per cent. Temperatures of 32° to 34° were unfavorable for percentage of eggs hatching but the length of the incubation period was very short. Higher temperatures destroyed the embryos. The minimum effective temperature for incubation of the eggs was about 10°. Relative humidities below 40 per cent were very destructive to the embryos.

The favorable region for larval development was between temperatures of about 20° to 30° C. with relative humidities ranging from 95 per cent to at least as low as 30 per cent. Temperatures above about 34° destroyed the larvae. The minimum effective temperature during the feeding period was near 10°, while that for the pupal period was slightly higher.

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HARDWOOD INVASION IN A COMPARATIVELY OLD WHITE PINE AFFORESTED AREA

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What will be the ultimate effect of biotic factors on developing forests is a problem of extreme importance in many of the eastern states where reforestation plans are rapidly being materialized. Especially is this true where areas or habitats not wholly adapted for certain desired conifer species are involved. At the present time we have attained a considerable knowledge relative to the effects of such biotic factors as plant succession, disease, insects and man upon forest production in natural habitats, but as yet little information is available relative to the rôle these factors play in afforested areas which have been allowed to revert to nature after years of careful forest management. With this problem in mind, the writer, in September, 1930, began a study of the effects of certain biotic factors in a small and comparatively old afforested area carrying a stand of white pines, *Pinus strobus,* which were in some cases approximately a century old. From general observations, it was apparent that hardwoods had invaded the stand with such rapidity and success that they threatened to become the dominant species in the near future. Furthermore, it was evident that the white pines were suffering a high mortality, due to biotic or edaphic disturbances.

In the course of the investigation, a number of quadrats were laid out and photographs were taken of the vegetation in order to secure data relative to the effects of the plant invasion in the pine grove over a long period of time. It was necessary to discontinue this study in November, 1931, when the city of Syracuse (present owner of the grove) found it necessary to eradicate the invading vegetation in order to prevent the partial or complete destruction of the white pine. The invaders, with the exception of a few cherry and maple trees, *Prunus serotina, P. avium* and *Acer saccharum* were removed and the habitat was rejuvenated in many low places by the addition of several inches of fertile soil. Before this change was made, considerable data were obtained which may throw some light on the problem mentioned above.

Historically, little is known of the original owner of the pine grove or of the date of the planting other than the annual ring history obtained from the trees. There are, however, two aged residents in the neighborhood who can recall several facts concerning the pine grove as it appeared and was managed 65 years ago. They state that there was at that time (1866) a pure stand of white pine averaging approximately 35 feet in height which provided adequate climatic protection for summer recreational activities. The grove was apparently well managed and free from hardwoods, with the exception of two or three basswood trees, *Tilia glabra,* until 1894, when it became the property of the city of Syracuse. Since 1894, the grove has been used for recreational purposes without silvicultural attention. When the city of Syracuse acquired this property, the Park Commission decided that silvicultural treatment was unnecessary because the trees appeared sufficiently large to control the future environment of the habitat. A brief study of figure 1, demonstrates how unwise the decision was and also illustrates the rapidity of plant invasion, once it begins. This fact becomes more striking when figure 1 is compared with figure 2, a photograph taken immediately after the removal of the plant invaders from the grove. The latter view is, no doubt, quite representative of the white pine forest floor as it appeared in 1894, but not of the crown growth which has been materially reduced since that date. Figure 3 shows an internal view of the vegetation of the forest floor during the late summer of 1931. This view demonstrates in a striking manner the ineffectiveness of the stand to control the invading vegetation as compared with the white pine stand[1] represented in figure 4; here the pines practically control the development of all plants in the habitat.

FIG. 1. The white pine grove as seen from a distance before the hardwoods were removed.

The habitat supporting the pine grove is not large, being approximately

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[1] A small habitat located at Cranberry Lake, N. Y.

200 feet wide and 250 feet long. It is situated on the southeastern outskirts of the city of Syracuse, New York, at the head of a small valley running southeast and northwest, surrounded by low rolling hills. Small areas of hardwoods as well as cultivated lands surround the grove on all sides. The soil is a well drained medium loam containing considerable calcerous material which has been transported by erosion from the immediate foothills rich in limestone. The soil is therefore slightly basic and shows an increased gradient with depth. The first two feet show a pH of 7.0 +; the third and fourth feet gave a pH of 7.2 and 7.3 respectively. It was impossible to obtain soil cores deeper than four and a half feet because of a limestone substratum. The thickness of the humus varied from a thin deposit to one inch in depth. Practically no needle duff was present on the surface, which may be accounted for by the severe pruning which the pines had received in the past. The chemical and physical properties of the soil in this area are highly differentiated as compared with the soil of natural habitats in the Adirondacks supporting white pine stands. In the latter, the soil is acid (pH 3 to 6.4) while below the needle duff, which varies from 1 to 3 inches in depth, is found a coarse sandy substratum.[2]

FIG. 2. The white pine grove immediately after the hardwoods had been removed.

The climatic conditions, with the exception of the air currents, are quite similar to those found elsewhere in the state where native white pine occurs. The grove is frequently swept by strong westerly winds which have deformed the trees (figs. 1 and 2). The top of each tree is bent toward the east and in a few cases as much as three or four feet of top growth is at 90 degrees

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[2] These data were obtained from a recent study made by the author of the chemical factors of the soil which influence the distribution of certain forest species in the Cranberry Lake region of the Adirondacks.

to the vertical position of the trunk. In many cases there are fewer branches on the windward side of the trees than on the leeward side. The dense shade of the hardwoods also caused the death of many large branches within the range of its influence. Many of these dead branches were removed during the eradication of the hardwoods and as a result only a small and high stand crown remains (fig. 2.) Such a small crown growth would certainly act as another limiting factor in the normal development of the pine stand. To what extent the wind has influenced the suppressed growth of the stand as a whole by dessication of the soil and the alteration of tree form, is not known. It becomes evident that the trees have been suppressed in growth when their diameters are compared with those of white pine of the same age in natural habitats in the Adirondacks. Insects, no doubt, played an important rôle in retarding the development of the stand, the pine weevil, *Pissodes strobi* Peck, being the principal offender. Several of the trees still show external evidence of weevil injury while others have no doubt suffered similar effects in the past which would now be concealed by subsequent growth.[3] During the insect attack the pines were apparently free from fungous diseases.

Fig. 3. The interior of the grove showing the dense growth of woody species resulting in the most severe type of competition.

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[3] MacAloney observed that white pine injury from weevil attack may become externally but not internally concealed by subsequent growth (N. Y. State Col. of For. Bull. No. 28, pp. 31–32, 1930).

In the foregoing discussion the more general features relative to the pine grove have been considered, and it is now pertinent to introduce more specific evidence as to the manner and the effects of the hardwood invasion. Quadrat studies clearly brought out the fact that black cherry, *Prunus serotina*, was the first hardwood species successfully to invade the pine grove. Increment borings taken near the base of the largest black cherry trees growing along the margins of the grove, gave evidence that the hardwood invasion began in 1897, approximately three years after silvicultural treatment had been discontinued. Hard maple, *Acer saccharum*, basswood *Tilia glabra*, and sweet cherry, *Prunus avium*,[4] did not become established until two years later but were more successful in distributing themselves throughout the grove than the black cherry. Only here and there in the more open places of the forest interior was the black cherry able successfully to compete with the above hardwoods. The advance of the hard maple during the interval of 35 years had been far more uniform over the entire habitat than that of either

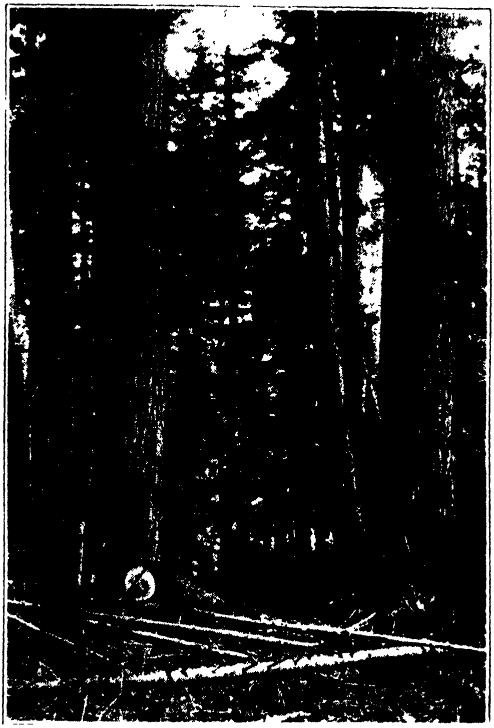

FIG. 4. A small stand of dominant white pine showing effective control by this species in the high mortality of hemlock and the absence of shrubs and herbs.

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[4] This is an escaped species. In many cases the exact age of this species could not be determined because of the decayed heartwood.

the basswood or sweet cherry. Whether such a condition was due to the species reaction to differences in light and soil or the summation of both is not known. Here the size of the afforested area seems to be a very important factor in the hardwood invasion because the hardwoods were able to advance from all sides without encountering a dense and heavy shaded interior so characteristic of large natural forests. Furthermore, the wind was able to penetrate deeply into the grove which would unquestionably aid in the invasion of the hardwoods by the dissemination of seeds from the parent plants along the margins. This would suggest that small areas are not as desirable for afforestation as large areas where hardwood invasion is a major consideration.

Notwithstanding the dense and rank growth made by the species mentioned above, many of the less sturdy harwoods such as dogwood, *Cornus stolonifera,* ironwood, *Ostrya virginiana,* and sumach, *Rhus typhina,* were able to survive and play an important rôle in the succession. Such shrubs as elderberry, *Sambucus canadensis,* and snowberry, *Symphoricarps orbiculatus,* were limited in their distribution to the immediate margins of the grove while the rose, *Rosa blanda,* and raspberry, *Rubus neglectus,* were abundant in the low depressions where lack of moisture was probably not one of the limiting factors. It was also in these low depressions that the most severe type of competition was going on between the subordinate woody species, and the maple and basswood seedlings. It is highly possible that the surface soil composed principally of deposition eroded from the higher levels contained slightly more available plant nutrients than the adjacent areas which may account for this dense undergrowth. In one of the two meter quadrats, 42 hardwood seedlings varying from six inches to three feet in height were growing among two large rose bushes and five medium sized raspberry bushes. One of the most striking observations made during these quadrat studies was the complete absence of white pine reproduction. This was likewise true of the immediate areas lying outside of the pine grove. It was also of interest to note that many dead clumps of both rose and raspberry species were distributed among the vegetation of the small depressions. These are no doubt the relics of a dominant vegetation which occupied the forest floor before the hardwoods successfully invaded the interior of the grove. Therefore, it would seem reasonable to conclude that the rose and raspberry bushes observed in the quadrats would also have met the same fate providing the competition had continued. Two small woody species, fox grape, *Vitis labrusca,* and poison ivy, *Rhus toxicodendron,* were very abundant in the grove. Because of their twining and climbing habit of growth, they were able to attach themselves to the trunks of the white pine and reach the more desirable light conditions. Here we find, as would be expected, morphological differences between the leaves growing in the light and those in the shade. The former were large and light green in color; the latter were small and dark green. The presence of poison ivy in this dense forest growth appeared to the writer at first to be an unusual case of a species growing out of its natural habitat since it is commonly found in the open areas attached to fence posts, rocks, and other supports.[5]

The herbaceous cover of the stand consisted primarily of a scattered growth of herb Robert, *Geranium robertianum,* and where the shade was not too dense a few individuals of ragweed, *Ambrosia trifida,* and two species of goldenrod, *Solidago canadensis* and *S. latifolia,* were present. This type of herbaceous cover expressed no correlation whatsoever in number or relationship of species with the herbaceous covers in natural hardwood stands or afforested conifer areas situated only a few miles from the grove. Such differences in vegetation highly indicate that plant heterogeneity of an extreme nature may follow a severe invasion reaction.

The root systems of the heterogeneous plant population of the grove offered a most excellent opportunity to study their physiological and ecological reactions upon the habitat. Only general observations, however, had been made before the hardwoods and shrubs were removed. A network of roots practically occupied the entire upper eight inches of the habitat which would indicate that the most severe type of competition was going on among the many species for the available plant nutrients of the soil. Mycorhiza were not as abundant, nor as highly developed on the rootlets of the white pine as were observed on similar organs of the same species carried by afforested areas free from hardwood elsewhere in the vicinity of Syracuse. This evidence is suggestive that the hardwoods and shrubs created by their root activities a soil reaction not whooly desirable for the normal production of these symbiotic forms. It is also highly possible that the reaction of the dense root systems of the invaders in the habitat played a primary rôle in upsetting the physiological balance of the white pine stand. As a result the white pine were unable successfully to compete for the desirable soil nutrients and their resistance was lowered. This is only a supposition, nevertheless here occurred an ecological problem which is associated with practically all stages of succession. To solve such problems should not be as difficult in the future as in the past with our present knowledge relative to the analytical and electrometric methods of analyzing the soil.

It is evident from the above data, as well as from figure 3, that the white pine grove began as a pure stand and had come to be a dense mixture of various species until silvicultural treatment was again resumed in the fall 1931. There were at this time 147 living white pine and 29 large stumps of the same species. The stumps were relics of the past since the Park Com-

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[5] W. L. Bray, Dean of the Graduate School, Syracuse University at Syracuse, N. Y., relates from his unpublished notes an interesting case regarding the invasion of poison ivy in the hardwood forests of southeastern Texas. The poison ivy grows up the tree trunks until it reached optimum light conditions, where it produces such an enormous foliage growth that it is difficult to recognize the species as the one so common in the open areas of the Northern States.

mission had the trees sawed down immediately after death. The annual ring count of the 29 stumps proved that the ages of these pines varied from 112 to 78 years old when they were felled. Eleven of these stumps were added to the list in the last two years. This high mortality sets forth in a striking manner the severe reaction of the invasion and also strongly indicates what the ultimate result might have been. Among the white pine were two individuals which were practically dead, and in order to eliminate any possible danger of the wind blowing them over and injurying healthy pine, they were sawed down during the early spring of 1931. If a study is again made of figures 1 and 2, it becomes obvious that the pine grove was given a pronounced opening up by the removal of the hardwoods. This may later constitute a severe shock to the stand with such a small crown and the possibility of an aftermath effect because of the hardwood reaction upon the habitat.[6] Therefore, additional deaths may occur among the white pine before they can adapt themselves to the new environment. This fact becomes more apparent when the scraggly white pine marked with an arrow in figure 2 are compared with the supposedly healthy individuals. As previously stated, the entire assemblage of trees shows abnormal development which may in part be attributed to the above causes.

Discussion and Conclusion

1. The data indicate in a highly definite manner the severe reaction of hardwood invasion in a small well-established afforested area not wholly adapted to white pine production. Notwithstanding, all the undesirable effects of insects, climate, and edaphic factors, the white pine were able to make fair growth for at least 50 years under silvicultural treatment, but when exposed to nature's competition the stand was unable to control the environment. The hardwoods, undoubtedly the most destructive biotic enemy of afforested conifer areas in New York State, made a successful invasion and threatened complete dominance.

2. The results of the present investigation as well as from observations and studies made in various regions of the Adirondacks clearly point out that certain natural areas in the State are more desirable for white pine production than other areas because of the differences of the soil complexity. We would therefore expect the same to be true for the hardwood species. From general observations and extensive series of determinations made by the writer in the Western United States, show that conditions similar to those mentioned above prevail and influence in a profound manner the distribution of vegetation in rather small and supposedly uniform areas. With these facts as guide criteria, those who contemplate reforestation or afforestation pro-

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[6] One of the largest pines of the grove was blown over during a rainstorm of April 7, 1932. This points out in a striking manner the results that may occur in the future due to the effects of the invasion and eradication.

grams should make not only a detailed study of climatic and topographical features of the site or habitat but also a detailed analysis of the soil as an aid in the propagation of species in order that those which require specific edaphic conditions may be grown successfully. If this procedure is employed in states where large areas of abandoned farm lands are to be afforested, a tremendous saving of time and money in forest production can no doubt be ultimately realized.

3. The data indicate that small conifer afforested areas do not afford as dense and heavily shaded an interior as is necessary for the checking of hardwood invasion. Larger areas would therefore be more effective as barriers to such an invasion.

REVIEWS

Braun-Blanquet's Plant Sociology[1]

The original edition of Braun-Blanquet's important " Pflanzensoziologie " appeared in 1927. Its translation began three years later and now the English edition is before us. It is more than a simple translation. As the preface states, the author has made changes in the German original, bringing the presentation up to date, and the translators have added some results of American work. There are still numerous moot points in associational ecology, and the translators state that in some portions the text expresses the opinion of the author rather than their own. It would be interesting to know just what those portions are. In preparing the review, no attempt has been made to check the accuracy of translation. The experience and ability of the joint editors and the cooperation of the author are sufficient assurance that the actual ideas of Braun-Blanquet are presented.

It is generally considered the duty of a reviewer to discover in a book numerous statements with which he disagrees, to call attention to these as flagrant examples of careless work, and to convey tacitly the impression that a much better book could have been written (ostensibly by the reviewer, although he never says so directly). I too have tried to find in this book statements which might be questioned. I have found some, to be sure, and shall mention them below, but every reader of the review will certainly see that they are few and unimportant and in no case detract significantly from the high value of the book as a whole. On the contrary, it impresses me as a highly valuable acquisition to ecological literature, covering the field clearly, adequately and authoritatively and discussing the more difficult subjects with remarkable freedom from personal opinion and bias. The translators must also be praised, for they have done their work so deftly that the book bears no appearance of having come from another language.

The plan of the book is unusual. In the first 73 pages the general nature and structure of the plant association are presented. The next 205 pages consider the environment. Then follow 16 pages on life-form, 36 on the development of communities, 15 on their distribution, and 16 on their classification. There are accordingly 156 pages which deal directly with associations in contrast to 205 pages devoted to the environment. A fine bibliography occupies 27 pages and the book closes with a comprehensive index of 33 pages. There are 42 tables and 180 figures, mostly in half-tone.

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[1] **Braun-Blanquet, J.** 1932. Plant Sociology, the study of plant communities. Authorized English translation of Pflanzensoziologie. Translated, revised and edited by **George D. Fuller** and **Henry S. Conard.** Pages xviii + 439. *McGraw-Hill Book Company, Inc., New York and London.* $4.50.

More than half of the book, therefore, deals with environment rather than with the association. There is no doubt that the effect of the environment is shown more clearly on the structure and behavior of the individual plant, and only indirectly on the association as the sum of the individuals. There are places in the text where the author seems to feel that his discussion is somewhat apart from the general subject of sociology, and some of his words may occasionally be construed as an apology. Nevertheless the whole treatment is clearly presented, readable and interesting, and being strictly modern is undoubtedly valuable.

In the chapter on life-form Braun-Blanquet adheres to the old system of Raunkiaer, with some modifications of his own, and his system is presented in detail. Other classifications are mentioned only incidentally; unfortunately the very recent work of Du Rietz was apparently received to late to get as much attention as it deserves. The author believes that life-forms are of only minor importance in characterizing associations, unless the number of individuals, mass, and coverage of each form is duly considered. Nevertheless they have a distinct value in preliminary or exploratory work, where an imperfect knowledge of the species prevents the use of a floristic basis. Vegetational units based on life-form are *synusia* and a combination of synusia is a *formation*. This may be a new approach to a definition of this time-worn term, but after all it differs very little from the original idea. The author thinks little of the value of such units; he gives them only a page in all, says they are used for "rough characterization" of vegetation, and can not be used as permanent bases in the nomenclature and taxonomy of communities. Here he is quite at variance with the opinion of Rübel. I believe most Americans will agree with Braun-Blanquet.

The principles of community development, which we Americans call succession, were first firmly established by Cowles and Clements. Braun-Blanquet apparently agrees with the ideas of Cowles, but severely criticizes those of Clements and his followers, stating that "the most exact ecological data remain sterile for sociological evaluations when assembled according to the system of Weaver and Clements." His discussion of succession presents little that is new, except possibly an elegant discussion of the effect of species in controlling succession (dynamogenesis) and an account of the use of pollen-statistics, but the whole treatment is fresh, suggestive and inspiring. Nevertheless, just when we think that his ideas are wholly untrammeled by conventional classifications, he introduces an arrangement of seres into nine groups.

The discussion of distribution of communities is also interesting. Horizontal (geographic variants) and vertical (altitudinal variants) changes in a community receive brief attention and the relation of such changes to the fundamental concept of the association is omitted. Zonation, migration and origin of communities are described. He then reaches the more general topic of world-wide distribution of vegetation and accepts very justly the conclusion of Drude and others that both floristic and sociological bases must be used. He recognizes six regional units, termed the region, province, sector, subsector, district, and subdistrict. Presumably the next lower step is the community complex or the association. His scheme is illustrated by European examples, but the value of the translation would be enhanced by the addition of American examples as well.

This is obviously one feasible method of classifying plant communities. It is based on the fundamental fact that associations occupy spaces, and their spaces are combined into units of higher order. In his next chapter he proceeds to another discussion of classification, first paying his respects to the " dynamo-genetic " system of Clements and the physiognomic system of Rübel. His own plan is based on similarity in floristic composition. A group of associations, each with its own distinctive species, but all with a series of species in common, is an *alliance;* alliances are united into *orders,* and they into *classes,* while the highest unit is the *circle of vegetation* and corresponds almost precisely with his *region* of the previous chapter. Braun-Blanquet's principle here is perfectly clear and remarkably like classification is systematic botany. He fails to make clear just how much or how little similarity in floristics is necessary for any of his groups. In this he again approaches the taxonomists, for they also can give no exact criteria for any of their classificatory units. Then he takes up a third method and gives a detailed table showing the various types of communities arranged according to their sociological complexity, beginning with aeroplankton and ending with a forest.

We recognize that the fundamental feature on which classification is based is similarity. Given a number of objects to classify, we can usually discover in them two or more categories of similarity and can make as many classifications. This author has chosen three of them, regional, floristic and sociological. He mentions and frowns upon two others, genetic and physiognomic. These two categories impress me as just as important as the regional and floristic viewpoints and are certainly far more tangible than the sociological. He is entitled to his own opinion, of course, and we other ecologists may follow him or Clements or Rübel, just as we please. But it is worthy of note that the regional and the floristic methods of Braun-Blanquet and the genetic method of Clements tend to converge on common ground at the highest group, while the physiognomic and sociological methods lead to entirely different results.

In presenting this review, I have purposely begun with the second part of the book. Having now reached the end, I turn back to the opening section, which in many respects is the most important part. We Americans think we know something about succession already and the classification of communities impresses us as rather theoretical, but all the recent European work on details of associational structure still seems a trifle strange to us. In the first short chapter, Braun-Blanquet describes the social life of plants, discusses competition, shows how the presence of a plant affects its neighbors, and tells us that some plants are far more aggressive than others. The last is of interest, for on it hangs his later development of the idea of succession. Unfortunately he leaves us with the idea that aggressiveness is an attribute of the species. *Elodea*, for example, is so aggressive that it overspread Europe with "the suddenness of an explosion." He apparently fails to realize that aggressiveness or timidity (if he can endow a plant with the one character, surely I can give it the other!) of any species depends on the environment. The water hyacinth is aggressive in Florida, as he says, but excessively timid in Montana.

Next he builds up his philosophical foundation for the concept of the association. This is a matter which must be approached with the utmost care. As long as we are dealing with concrete tangible entities, we can say many true things about them, even though our fundamental concepts are wrong. But the association is a concept and we must be careful that we understand its *raison d'etre*, its *ultima principia*, its *Sein und Wesen*, if we are to arrive at a correct expression of its scope and structure and later of its origin, history and classification.

"The ultimate 'atomistic' particles of a community," says Braun-Blanquet, "are the individual plants. The combination of these creates the social organism." Right: but I assume he did not mean organism in the sense in which it was used some years ago by Clements, since he distinctly disavows that idea elsewhere in his book. Note that he uses the word *combination* rather than *classification*. "The countless individuals may be grouped in two distinct ways, under the concept of the taxonomic species or under the concept of the growth forms." By *grouped* he undoubtedly means *classified*, since the process leads to a concept. Growth form "can not be considered as a sufficient basis for a science of vegetation." Braun-Blanquet must necessarily take this stand, because, as mentioned above, he later in the book denies the classification of associations on this basis. Species can be so used, according to the author, and are taken by him as the basis for his floristic concept of the association. "Pieces of vegetation" (*Einzelbestand*) "with similar combinations of species are united into abstract types," the association. While the author does not say so definitely, and while the quotation in the preceding sentence may be construed to the contrary, the impression is clear that he attempts to *combine* the abstract concepts of species into the concrete entity, the *Bestand*. Such a procedure is of course logically impossible; concepts can never be combined into concrete entities. No further definition of the association is attempted and just how much floristic similarity is required or how much floristic difference may be tolerated is not stated. In fact, I doubt if the author could make a statement in any definite terms.

Little help is given us for the development of a practical concept of the association in the field. We are told that we must not rely on quadrat studies and are advised that every stand of the association must include the essential characters of the association, and again that the stand "embodies in itself the distinctive marks of the association." Elsewhere he says that the definition of the association (meaning the formation of an association-concept) requires skill, sociological training, and wide experience. Probably the readers of this review, being gifted with these valuable attributes, approach such a task confidently, but I doubt if many of them will feel sure that their results are precisely the same as those which Braun-Blanquet would have attained.

Passing on to the next chapter, he discusses the structural characters of the community, including abundance, density, cover, gregariousness, frequency, layering, vigor, and periodicity. Nothing new is presented here, but the matter is relatively new to American literature and is treated with a clearness that is delightful. Some suggestions are made on the methods of observing and recording structure, but only in the most general terms; the book does not pretend to be a field manual. Another chapter, the last one we have to consider, takes up the more abstract characters of the association, distinguished as presence and fidelity. The former refers to the regularity of occurrence of a species in all stands of the association and entails a discussion of minimal area and the relation of species and area; the latter refers to the limitation of species to one association only (indicator species). These complex subjects are discussed with sufficient fullness for a textbook, and the numerous references serve as a guide for the research ecologist.

It is easy to use much space for criticism, while commendation requires but a few lines. In conclusion, lest it be inferred that my criticism outweighs my praise, may I ask that my readers turn again to the second paragraph of this review?

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THE NEW YORK BOTANICAL GARDEN

ECOLOGICAL LITERATURE RECEIVED

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NOTES AND COMMENT

SOIL TEMPERATURES AND EVAPORATION IN A PAPER BIRCH-WHITE PINE FOREST, LONG LAKE, HAMILTON COUNTY, NEW YORK

The following data were obtained during the summer of 1932 in a 50-year old stand of paper birch, *Betula papyrifera* Marsh., and white pine, *Pinus strobus* L., on the northern shore of Long Lake, Hamilton County, New York, at an altitude of 1640 feet. The open station was located in a small opening about 200 feet back from the lake shore and 25 feet above the lake surface. It was exposed to full overhead light and to the sun about seven hours a day. The woods station was located 500 feet farther inland under a complete canopy of paper birch, white pine and balsam fir, *Abies balsamea* (L.) Mill.

Soil temperatures were measured by ordinary chemical thermometers enclosed in hollow wooden stakes provided with ventilation holes opposite the thermometer bulbs. The stakes were driven in vertically until the position of the bulb was one foot below the surface. The exposed part of the stake was painted white, and the cork from which the thermometer hung fitted into a projecting white wooden cap.

TABLE I. *Weekly averages of temperature in degrees Fahrenheit, evaporation in cubic centimeters per week*

Dates 1932	Open				Woods	
	Rainfall inches	Air temp. 7 A.M.	Soil temp.	Evap.	Soil temp.	Evap.
June 27 to July 3....	0	—	59.1	93	54.3	53
July 4–10..........	3.12	57.9	59.2	70	53.0	28
July 11–17.........	0.41	56.8	62.0	115	55.1	58
July 18–24.........	2.67	56.5	63.0	96	55.6	45
July 25–31.........	2.62	58.8	63.3	75	56.4	17
August 1–7.........	1.21	57.9	62.7	80	56.4	18
August 8–14........	1.46	56.3	62.4	72	57.5	33
August 15–21.......	1.18	57.7	62.3	76	56.5	22
August 22–28.......	.78	56.3	62.0	72	56.5	37
Totals.............	13.45	458.20	556.0	749	501.3	311.0
Averages...........	1.49	57.2	61.8	83.2	55.7	34.5

Evaporation was measured by standardized Livingston spherical atmometers, exposed six inches above the soil. They were fitted with Livingston-type non-absorbing mountings and filled with distilled water. The atmometers were filled at weekly intervals, and soil temperatures were read at 7 A.M. daily. At the open station air temperature and rainfall were also recorded daily at the same hour.

Evaporation followed much the same trend within the forest and in the open during the first half of the summer, but thereafter the relation was reversed. There was obvious connection between rainfall and evaporation, but no direct relation between evaporation and soil temperature was apparent.

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THE EFFECT OF THE 1932 ECLIPSE UPON THE WIDTH OF STOMATAL OPENINGS IN GRAY BIRCH

The opening and closure of stomata are controlled by a complex of factors, one of which is light. Lloyd,[1] Loftfield,[2] Scarth,[3] and others have carried on extensive studies in this field. The 1932 eclipse offered a unique opportunity for the study of the effect of light upon the stomatal mechanism.

The study was made on the Yale Forest at Keene, N. H. Keene is located in the southwest corner of New Hampshire approximately forty miles from the zone of total eclipse. Microscopic measurements of the width of the openings of the stomata of gray birch, *Betula populifolia* Marsh., were made at fifteen-minute intervals on August 31, 1932, the date of the eclipse, the first measurement being made at 2:15 P.M. and the last at 5 P.M. The number of stomata measured each quarter hour varied from 26 to 52.

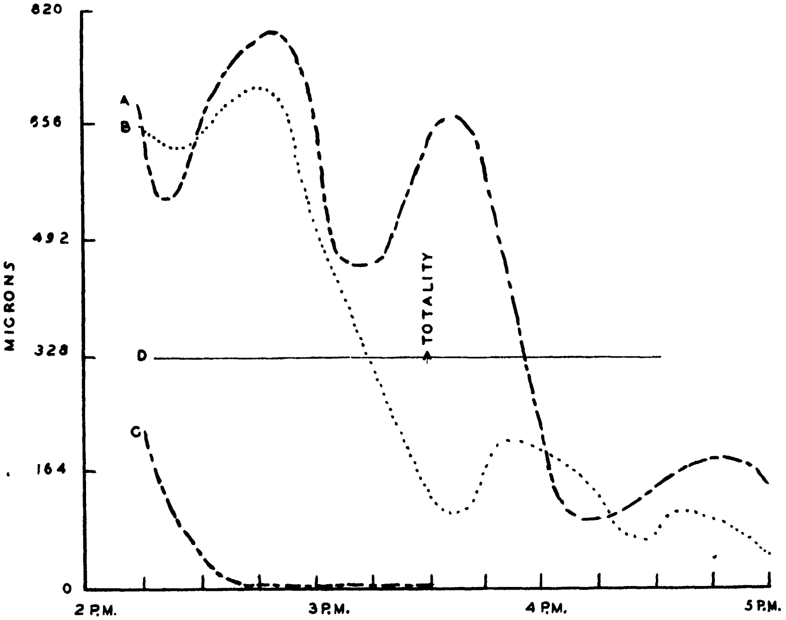

FIG. 1. Diurnal variation in width of stomatal openings on September 4 (*A*), August 31 (*B*), and September 6 (*C*). Duration of the eclipse (*D*).

The procedure followed was in general much after that of Stålfelt.[4] The result of these measurements is graphically presented in figure 1.

For comparison, measurements taken on September 4, 1932, and September 6, 1932, are also presented. September 4 was chosen because the weather was quite similar to that of August 31. September 6 was chosen as representative of a bright, sunny day.

[1] **Lloyd, F. E.** 1908. The physiology of stomata. . *Carnegie Inst. Wash., Pub.* 82.

[2] **Loftfield, J. V. G.** 1921. The behavior of stomata. *Carnegie Inst. Wash., Pub.* 314.

[3] **Scarth, G. W.** 1932. Mechanism of the action of light and other factors on stomatal movement. *Plant Phys.*, 7: 481–503.

[4] **Stålfelt, M. G.** 1929. Neure Methoden zur Ermittlung des Öffnungszustandes der Stomata. *Handbk. Biol. Arbeitsmeth. Abderhalden. XI.*, 4: 167–191.

The weather conditions on these days at 2 P.M. were: August 31, relative humidity 65 per cent, air temperature 75° F., sky overcast all day; September 4, relative humidity 68 per cent, temperature 74°, sky overcast all day; and September 6, relative humidity 62 per cent, air temperature 80°, sky bright and sunny.

The leaves were selected from the same tree on August 31 and September 4. On September 6 the leaves were taken from a nearby tree of approximately the same environment, size and vigor. In each instance, leaves were taken at approximately the same distance above ground.

According to Slocum[1] the eclipse began at 2:19 P.M., reaching the total phase at 3:30 P.M. and ended at 4:33 P.M.

On August 31, the stomata began to close at 2:45 P.M. or about 25 minutes after the beginning of the eclipse. The low point was reached at 3:35 P.M. which was followed by a slight opening. In contrast to this the stomata were well open at 3:35 P.M. on September 4. The measurements which picture the openings on September 6 show the stomata to have closed at 2:30 P.M. The course of stomatal openings as portrayed for September 6 is characteristic for gray birch on bright, sunny days at Keene, N. H.

From this study it appears that the stomata of gray birch were influenced by the light conditions of the eclipse.

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[1] **Slocum, Frederick.** 1932. The total eclipse of the sun of August 31, 1932. *Science,* 76: 135.

ERRATA

VOLUME XIII, No. 4, 1932

p. 336, fig. 1. Transfer this graph to fig. 6. This is the graph of the rhythmic activity of *Boletotherus cornutus* in total darkness.

p. 341, fig. 6. Transfer this graph to fig. 1. This is the graph of the nocturnal activity of *Parcoblatta pennsylvanica* under relatively normal conditions.

ECOLOGY

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BOTTOM SHORE FAUNA OF WESTERN LAKE ERIE: A POPULATION STUDY TO A DEPTH OF SIX FEET[1]

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Introduction

Lake Erie has long been reputed to be the most thickly populated of the Great Lakes and there are at least two important reasons why this should be true; one being that the lake is generally shallow, another that it is correspondingly warm. At the time this study was begun practically nothing had been done in the way of a systematic investigation of the quantity of life in the lake, although of course the importance of its commercial fisheries indicated an abundance of invertebrate food. Quite recently the bordering states and the Federal Government have conducted a joint survey of the fish in the lake. So far as the bottom conditions are concerned their work has been confined to the off shore and deeper regions, that is, to depths greater than six feet. We limited ourselves to depths of six feet and less because preliminary observations made by the senior author, in the course of field work with classes at the Stone Laboratory, indicated that the greatest variety of species and the largest number of individuals occurred within such depths. This seemed, therefore, to be the natural line of separation from a general investigation of the lake bottom which we were not prepared to undertake. The study has been confined to the western portion of the lake since it was impossible to cover the entire lake, and the western region happened to be most accessible to the Stone Laboratory. Incidentally this western end, because of the number of its islands, affords the greatest amount of shore line and the widest variety of shore conditions. These conditions together with its shallowness and consequent warmth make it particularly rich in bottom fauna. No attempt has been made to study the entire shore line of the region.

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[1] Paper No. 4 from the Department of Biology, Ohio University, and a contribution from the Stone Lake Laboratory of Ohio State University.

The aim has been rather to select the chief types of shore and to study the relation of shore conditions to the abundance and distribution of the animals present.

The types of shore selected were the following: rock cliff with submerged boulders and rubble, shelving rock, rubble beach, rubble bar, pebble beach, bare sand beach, hard clay *Scirpus* beach, hard clay *Scirpus-Potamogeton* beach, *Scirpus-Potamogeton* sand beach, *Potamogeton* sand shoal. All of these situations, with a single possible exception, represent conditions in the open lake, that is, they all lie in positions which are exposed to the general sweep of lake waters. The possible exception is the rubble bar, which lies in Put-in-Bay harbor, but even this situation is not comparable to that of the semi-detached bays, lagoons, and marshes which are abundant along the southern shore of this western end. These semi-detached waters are, of course, biologically an intrinsic part of the lake and must be considered in any complete analysis of the lake shore. However, they are so extensive and so varied in nature that for purposes of study they form a unit in themselves and have not been included here.

Since the size and character of stones, forming the substratum, constitute a leading feature of certain beaches it seems desirable to define the descriptive terms applied. Such terms as gravel, rubble, pebble, rocks and stones are in common use. Of these, rocks and stones are useful merely in making generalized differentiations. The terms gravel, rubble, and pebble lend themselves to more detailed distinctions but unfortunately there appears to be

FIG. 1. Rubble Beach. The stones commonly found on this type of rubble beach are irregular and angular in appearance.

confusion in their use. We have applied the term rubble to beaches covered with coarse, angular or water worn pieces of stone of miscellaneous size and shape (fig. 1). In general, their dimensions varied from 1 x 2 x 3 inches to 2 x 4 x 8 inches or even larger. The designation pebble beach has been used for stretches of shore covered with small, smooth, well-worn stones, the dimensions of which are frequently ½ x 1 x 1½ inches, although marked variation exists as will be seen from fig. 2. By a gravel beach we have meant one covered with a mixture of pebble-sized stones and sand. Shelving rock beaches are those composed of broad sheets of solid rock having a gradual angle of submergence (fig. 3).

FIG. 2. Pebble Beach.

The study was planned and begun by the senior author and later completed with the assistance of the junior author during the summer of 1930. The junior author should not be held responsible, however, for any errors of

FIG. 3. Shelving Rock Shore.

omission or commission that may have occurred. Both of us are indebted to Mr. C. J. Munter, chemist at the Stone Laboratory, for assistance in making analyses and to Mr. C. A. Dennis, a student, for field assistance. Without the facilities of the Stone Laboratory which were placed at our disposal the work could not have been undertaken.

METHODS

A number of studies of the population of lakes have been made by various limnologists but, as a rule, they have discussed that region to which our study is limited under such general designations as the shore zone, the rachion region (Muttkowski, '18) or the shallow water area (Baker, '16). Since these regions are by no means a unit either in their physical conditions or in their biotic organization and, furthermore, since their limits have been determined by no common standard, we felt that a more detailed analysis of the population based on definitely determined depths would give a better conception of the actual conditions and afford a more accurate basis for comparison. We have, therefore, selected four depths or contours for detailed study at each of the habitats.

These depths are (*a*) from water-line to six inches, (*b*) eighteen inches, (*c*) thirty-six inches, and (*d*) seventy-two inches. The choice of these was partly an arbitrary matter and partly determined by conditions such as the amount of silt and vegetation present. A more detailed characterization will be considered later in another connection.

The results dealing with total population and species distribution at each habitat are based on the study of one square yard of the substratum at each level. In the case of stony substrata the method employed in making the census was to pick up by hand each stone in the area, examine it and record the animals found. At the six foot depth the stones were obtained by means of a grapple made of two long handled rakes fastened together so as to work on the principles of oyster tongs. This method was probably a source of error because a few of the more active and sensitive forms very likely dropped off, although observations made over a number of years give rather uniform results. Occasionally also, not all of the stones within an area could be grappled. To meet the latter difficulty the proper area was marked off on the deck of a boat and filled with stones taken, as far as possible, from the selected area but, if necessary, from outside this area. The extremely small stones which frequently lay under the larger ones were washed in a net to obtain the forms adhering to them. On sandy substrata, the sand was either scooped up in a dip net or dredged, depending upon the depth of the water. Bare hard clay bottom was scraped with a flat edged dip net. All this finer material was washed through a sieve and even examined by hand, if necessary.

In the treatment of vegetation, *Potamogeton* and similar leafy forms were torn loose by hand or by means of the grappling rakes. They were then washed in three separate waters and the water was then passed through a sieve. Here again a few forms may have been lost in the washing or as the plants were drawn to the surface. *Scirpus* was pulled up by hand and each stalk examined separately. *Cladophora* was washed in the field and also examined in the laboratory.

Temperature was obtained by means of a Negretti-Zambra reversing thermometer. pH was determined colorimetrically. For carbon dioxide and oxygen the standard methods of water analysis were followed, the modified Winkler method being used for oxygen.

RESULTS

Physical Factors

In general the data assembled show that the abundance and variety of animals along the shore of the lake is closely correlated with the nature of the substratum. It should be noted in this connection that a given type of substratum implies certain fundamental conditions, such as exposure to wave action, slope of the bottom and other concomitant conditions. For instance, a bare shelving rock substratum is most likely to occur in a situation exposed to severe wave action, since otherwise the rock would shortly be covered with accumulations of various sorts which would make an entirely different habitat.

Other factors considered, such as temperature, gaseous content and pH, showed no variations which were significant in relation to either the numbers or the variety of animals present. Temperatures at widely separated places show close uniformity, and similar uniformity is evident when thinly populated and densely populated localities are compared. For example, a well inhabited boulder bar in mid-lake had an August temperature of 22.5° C., a sparsely populated pebble beach had a temperature of 22° C., and a clay shore intermediate in degree of population had a temperature of 22.1° C. Temperatures of 24°, 25°, 25.2° C. occurred after prolonged warm weather at an almost barren sand beach, a well populated shelving rock shore, and a moderately populated *Potamogeton* sand shoal. The average of pH determinations taken at ten day intervals during July and August was 8.38 at a shelving rock shore exposed to the open lake and 8.42 at a partly protected rubble bar a few miles away. Determinations taken during August at a sandy shoal, a rubble beach, and a gravel beach were pH 8.2, 8.1, and 8.0 respectively. Oxygen determinations scattered over intervals of a few weeks from July to October gave average results of 8.22 p.p.m. on a shelving rock shore, and 7.74 p.p.m. at a protected rubble bar. At these same places carbon dioxide determinations taken in July and again in August gave the following average results: rock shore free CO_2, 3.33, fixed 39.48; rubble bar free CO_2, 2.13, fixed 40.23. A set of determinations is given in table I covering the factors of pH, free and fixed CO_2, oxygen, and temperature, all taken during the mid-day hours of the same day at several different stations and at each of the depths studied. Here again, the results do not run parallel with density of population.

TABLE I. *Results of determinations made during the mid-day hours of a single day (September 11, 1930) at several widely separated points, regarding the temperature, dissolved oxygen, free and fixed carbon dioxide, and pH, for each of the depths considered.*

Station	Depth Inches	Temp. C.	Oxygen p.p.m.	Carbon Dioxide Free p.p.m.	Carbon Dioxide Fixed p.p.m.	pH
Flat Rubble.	6	20	9.52	−2.4		8.2
	18	20	9.54	−1.7		8.1
(Sugar Island).	36	20	9.16	−1.7		8.1
	72	19	8.65	−0.93		8.1
Pebble Beach.	6	20	8.33	0.0		8.0
	18	20	8.21	−1.6	37.0	8.0
(N.W. Middle Bass).	36	20	8.76	−1.4	37.8	8.1
	72	19	8.51	−0.42	40.0	8.0
Irregular Rubble.	6	20.5	8.62	−0.42		8.1
	18	20.5	9.17			
(Burn's Dock).	36	20.5	8.30	−0.84	38.8	8.1
	72	20	8.32	−0.75	38.9	8.1
Shelving Rock.	6	22	9.90	−4.8	38.4	8.8
	18	21	10.0	−3.7	38.5	8.6
(Buckeye Point).	36	21	9.60	−3.4	39.0	8.6
	72	21	10.0	−3.5		8.6
Protected Rubble Bar.	6	22.5	11.6	−6.5	38.7	8.8
	18	22	11.0	−5.5		8.8
(Alligator Bar. Inside of Tip considerable vegetation present).	36		11.3	−4.9	39.1	8.8
	72		12.4	−5.3		8.8

Population and Substratum

The relation between population and type of substratum is shown as a graph in fig. 4 with respect to the population found strictly on the bottom and not on vegetation; sandy beaches and shoals with an average population of

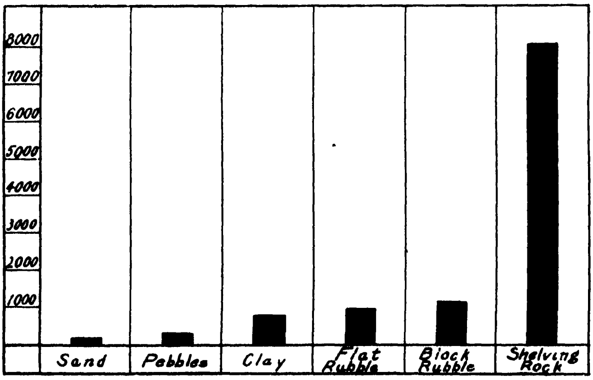

FIG. 4. Total population in relation to the type of substratum. The figures indicate the population per square yard in thousands.

about 100 individuals to the square yard are the most sparsely inhabited. Pebbles, hard clay, flat rubble and angular rubble follow in order of increasing population, the rubble having a population of approximately 1100 individuals to the square yard. A rather surprising result is the fact that flat, shelving rock is the most densely inhabited of the substrata with a total average population of 7700 individuals. This total is largely due to the great numbers of midge larvae as shown in fig. 4. The relatively smooth, flat sheets of rock characteristic of this type of shore (fig. 3) are generally found in exposed situations where storms keep them swept bare except for a narrow zone near the water's edge which may become richly covered with *Cladophora*. With the exception of the midge larvae, whose cases were securely fastened to the flat rock, more of the population was confined to this zone where the shallowness of the water and the *Cladophora* together ameliorated the sweep of the waves.

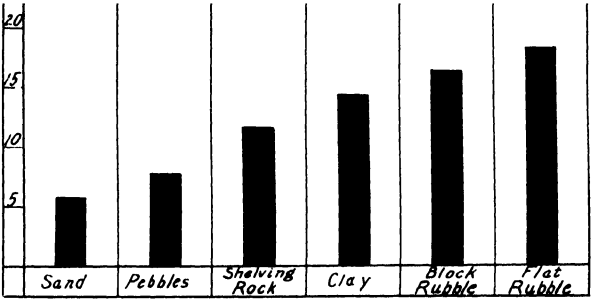

FIG. 5. Number of different kinds of animals per square yard on different types of substrata.

If one considers population from the standpoint of the variety of forms inhabiting a given substratum the results are quite different. This is evident from the graph given in fig. 5. The number of forms steadily increases as one passes from a less stable substratum to one that combines stability and protection. Bare solid rock affords the maximum of stability but little in the way of shelter. A flat-rubble beach appears to present optimum conditions (fig. 6). Flat stones are not easily rolled about and, therefore, when piled one upon another they provide a maximum of protected surface per unit area. Area for area angular rubble provides as much surface as the flat rubble does, if not more, but it is more easily disturbed. Hard clay by itself is very nearly as stable as flat rock and like flat rock it can be swept bare by waves. When dotted with stones, as in the case of a clay-rubble substratum (fig. 7), it affords more foothold and better protection than that given by flat rock. Pebble beaches and sand beaches leave little to choose between them so far as stability and protection are concerned. The constantly rolling pebbles and the constantly rasping sand are about equally unfavorable. How-

FIG. 6. Flat Rubble Beach. A type of rubble beach on which flat stones make up an important part of the substratum.

ever, the character of the deeper zones of the pebble beach merges with that of deeper zones of more favorable substrata, whereas this is not ordinarily true of a sandy bottom. For this reason the studies along pebble shores showed a greater variety of forms than those on sandy beaches.

FIG. 7. Clay-Rubble Beach. A hard clay beach over which rubble is scattered.

Population and Vegetation

Up to this point the discussion has applied only to animals actually living on the substratum. It has not included those that inhabit the vegetation. These animals must, of course, be included in any picture of what a habitat can support but they can scarcely be used in making comparisons between different substrata, since their dependence upon the substratum is only indirect and, furthermore, since the vegetation is not unfailingly present. The results derived from an examination of the vegetation are given graphically in figures 8 and 9. No attempt has been made to differentiate between the various kinds of leafy, rooted vegetation such as *Potamogeton*, *Myriophyllum*, and *Ceratophyllum*. All of it has been grouped together under the heading of *Potamogeton*. The hard surfaced, non-leafy vegetation is almost entirely *Scirpus*. The only other type of vegetation considered was the alga *Cladophora*, which grows in clumps along the shore or is found clinging to other vegetation.

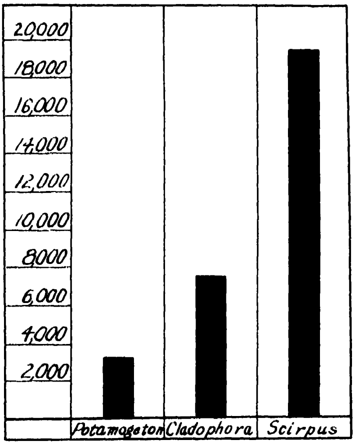

FIG. 8. Relation between the character of the vegetation and the total population. The figures indicate population in thousands per square yard of substratum area covered by plants. The large total population found on *Scirpus* is due to great numbers of chironomid larvae on these plants.

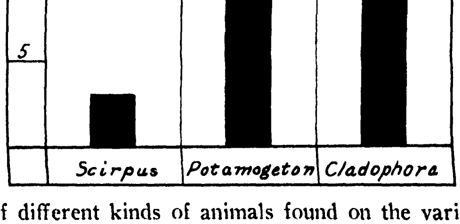

FIG. 9. Number of different kinds of animals found on the various kinds of plants.

Scirpus is ordinarily reported to be unsuited to animals (Shelford, '13) because of its smooth, hard, non-leafy surface. This has held in our results so far as variety of forms is concerned (fig. 10), but it does not hold in the matter of total population. In this respect *Scirpus* leads all other types of vegetation (fig. 11), a condition which is due to the almost unbelievable numbers of midge larvae which attach their cases to its surface. It was not at all unusual to find the stalks completely covered with the cases for several inches below the surface of the water. On the other hand, so far as variety of forms is concerned, *Scirpus* is completely outranked by both *Potamogeton* and *Cladophora*. Each of these were inhabited by 11 different forms, which is practically four times the number found on *Scirpus*.

Vertical Distribution

An analysis of the vertical population developed the fact that both in total population and in number of forms the eighteen inch contour is foremost (figs. 10, 11). With respect to total population, the high average for this depth is due primarily to the presence of large numbers of chironomids on shelving rock. The six inch and the thirty-six inch contours are about equally well inhabited whereas the seventy-two inch contour is the least populous. Although the eighteen inch contour has the greatest variety of forms, there is, in fact, little difference between the various depths except for the thirty-six inch contour which has notably fewer forms.

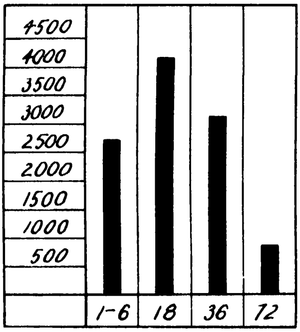

FIG. 10. Total population per square yard at each of the depths. Depth is indicated in inches at the bottom of the graph.

Animals Represented

So far the discussion has concerned itself with the distribution of totals, total population and total number of forms. The distribution and relative abundance of the various types of animals present with regard to depth, type of substratum and vegetation are presented in table II. Since our attention has been directed mainly to the density of population, the identifications have

TABLE II. *A list of the genera (in a few cases families merely) found in the course of the investigation. In columns to the right indications are given of the occurrence of the different forms and their abundance per square yard under various conditions. x = present, xx = numerous, xxx = maximum. The number of forms indicated for various substrata includes animals found on vegetation as well as on the substratum proper.*

Animal	Depth in Inches				Type of Substratum						Vegetation		
	1–6	18	36	72	Sand	Gravel	Shelving Rock	Clay	Flat Rubble	Angular Rubble	Scirpus	Potamogeton	Cladophora
ANNELIDA													
Limnodrilus			x	x	x			x					
Nais	xxx												xxx
Lumbricillus		x											
Placobdella				x				x					
Herpobdella	xxx	xx	x	x		x		x	x	xxx			
Glossiphonia	xxx	x						x		xxx			
ARACHNIDA													
Hydracarinids	xx	xxx	x	x		x		xx	x	xxx		xx	x
BRYOZOA													
Plumatella	x	xx	xxx	x		x			x	xxx	x		
COELENTERATA													
Hydra	x	xxx	x	x		x			xx	xxx			
CRUSTACEA													
Gammarus	xxx	xx	x	x	x			xx		xxx		xx	xxx
Hyalella	xxx	xx		x	x				x	xxx			x
Cambarus	xxx	x				x		x		x			
Asellus		x								x			
INSECTA													
Chironomid Larvae	xx	xxx	x	x	x	x	xxx	x	x	xx	xxx	xx	x
Hydroptilidae	xxx	xx	x	x	x	x	x	x	xx	xxx	x	x	
Leptoceridae	xxx	xx	x	x	x	x	x	x	xx	xxx	x	x	
Hydropsyche	xxx	xx	x	x		x	x	x	xxx	xx			
Helicopsyche	xxx	x	xx	x	x	x	x	x	xx	xxx			
Ryacophilidae	x	xxx	xx	x					x	xx			
Molanna				x		x							
Sericostomatidae		x							x				
Caenis	xx	xxx			x	x	x	x		xxx		x	x
Hexagenia		x							x				
Heptagenia	xx	xxx			x	x	x	x	xx	xxx			
Ameletus	x	x		x	x							x	x
Parnidae (Adults)	xxx	xx	x	x	x			x	x	xxx			
Atherix	x				x								
Corixa	x				x								x
Zygoptera				x	x								
Perla	xxx	x								x			
MOLLUSCA													
Amnicola	xx			xxx	xxx				x	x			
Goniobasis	xx	x	x	xxx	x	x	x	x	xx	xxx			
Physa	xxx	xx	x	x	x	x	x	x	xxx	xx			
Pleurocera		x	x	x	x				x	x			
Campeloma		x	x		x					x			
Lymnaea	xxx	xx		x			x	x	x	xxx			
Planorbis	xxx	x					x		x	x			
Ancylus				x			x						
Segmentina				x						x			
Lampsilus		x			x								
Pisidium				x	x								
Bythinia				x	x								
PORIFERA													
Spongilla	x	x	xx	xxx			x		xx	xxx			
TURBELLARIA													
Planaria		xxx	xx	x	x	x		x	x	x			

not been as detailed as they might otherwise have been. We have not attempted to follow the distribution of individual species. Indeed, this would have been impossible in the case of some of the insects, since most of the insects were larvae and in certain instances the species of larvae are not known.

A total of 44 groups were distinguished, 37 of these being genera and 7 of them families. Of these, slightly more than a third, seventeen to be exact, are insects and approximately one fourth (12) are mollusca of which nine are snails.

A noteworthy feature of the distribution is the fact that the only forms to be found everywhere were caddis fly larvae and midge larvae. These were on every type of substratum at every depth and, with one exception, on all forms of vegetation. Next to these in the extent of their distribution come the two snails, *Goniobasis* and *Physa*, which were found everywhere except on the vegetation. In view of this, the bottom dwelling population of Lake Erie to a depth of six feet can be termed a midge-caddis-snail association. In point of numbers the chironomids were the dominant animals. It will be noted that both the snails and the insects were abundant on at least two different types of substrata and at two different depths. The chironomid larvae were most abundant on shelving rock and *Scirpus*. It may or may not be significant that both of the latter represent the firmest substratum in the type to which each belongs, namely the lake bottom and the vegetation. However, the chironomids were not much less abundant on rubble and *Potamogeton*. The midges and the caddis larvae were both more numerous at the six inch and the eighteen inch depths than at other depths. The caddis larvae were present in greatest numbers on rubble. This is true also of the snails.

Other forms found at all depths, although not generally distributed otherwise, were the leech *Herpobdella*, the hydracarinid mites, the bryozoan *Plumatella*, the common *Hydra*, the amphipod *Gammarus*, the freshwater sponge *Spongilla*, and adult parnid beetles. This adult insect wandering about under water to deposit its eggs even at a depth of six feet was one of the most interesting animals of the shore. It, together with *Herpobdella* and *Gammarus*, was present in greatest numbers within the six inch contour.

With respect to abundance, it should be noted that more forms, in fact twice as many (15), were found in maximum numbers within the first six inches of water than at any other depth (table II). Seven forms reached their maximum at eighteen inches, 3 forms (*Amnicola, Goniobasis* and *Spongilla*) at seventy-two inches, and only 1 (*Plumatella*) at thirty-six inches. These facts, particularly the fact that so many animals are at their maximum in the six-inch zone, may not seem to harmonize with the data presented in fig. 10. However, the figure deals with total population and this, as was pointed out, is due to large numbers of a single group, the chironomids, whereas table II indicates maximum numbers for the respective animals which does not necessarily mean large numbers in an absolute sense. The abundance, in actual numbers, of a few of the genera commonly found is shown by graph in figures 11 and 12.

Since so many animals are present in maximum numbers within the six inch contour it would indicate that this depth represents optimum conditions for shore forms. This result is interesting in view of the marked similarity shown in table I between certain physical factors at all depths, although, of course, the table does not necessarily represent conditions over a long period of time. Evidently other factors must be considered in explaining the results.

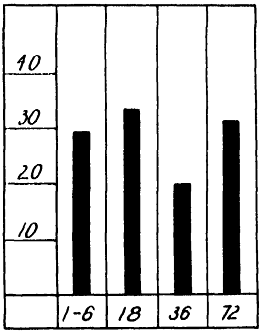

FIG. 11. Number of different kinds of animals that occur at depths considered. The depth in inches is indicated at the bottom of the graph.

Among the conditions worthy of attention in reaching an explanation are fluctuations in water level, wave action, and the amount of sediment present (fig. 13). Considering these points, we find that in the region between the surface of the water and the six inch contour, fluctuations in water level are most noticeable. Two factors making for this are the seiches and the tides. Both of these normally cause a three to four inch difference in the depth of water (Krecker, '31), the tides at the usual intervals of twelve hours and the seiches at intervals ranging from as short a period as fifteen minutes to an

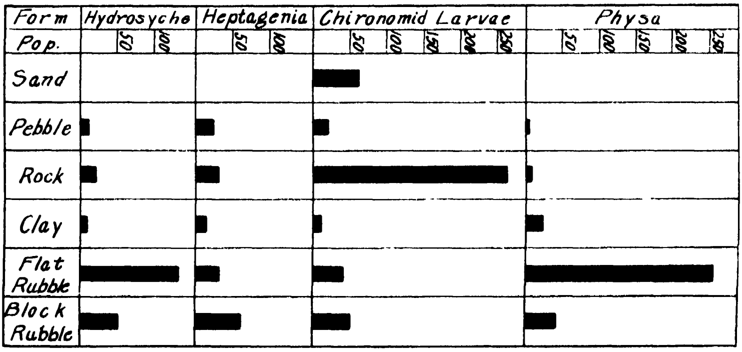

FIG. 12. Total number of individuals of certain forms per square yard on different types of substrata. The number of chironomid larvae is reduced 9/10.

hour or even several hours. Consequently the depth of water within the six inch contour fluctuates at frequent intervals from a maximum of six inches to a temporary depth of two inches at its deeper limits, and to no water at all over its shallower parts. This zone is further characterized by the constant lapping of water even on the calmest days, and by the consequent absence of an accumulation of sediment. In terms of plants it is the *Cladophora* zone, where conditions are suitable for the growth of this alga. The eighteen inch contour is not so seriously affected by the ordinary fluctuations of the water and animals living at this depth are constantly covered. It is shallow enough, however, to enable ordinary waves to provide a marked movement of water over the substratum and there is, in consequence, only a slight trace of sediment. At three feet, a strong washing effect from waves occurs only during rough weather and sediment may be pronounced. The six foot region is markedly disturbed only in time of unusually severe storms and, therefore, it normally presents a minimum of water movement and a maximum of sediment. Both water movement and sediment have an important bearing upon suitable conditions for respiration. Possibly then, since the vertical distribution of oxygen is good, one reason for the relatively low total population of the six foot contour may lie in the clogging effect of sediment upon the respiratory surfaces.

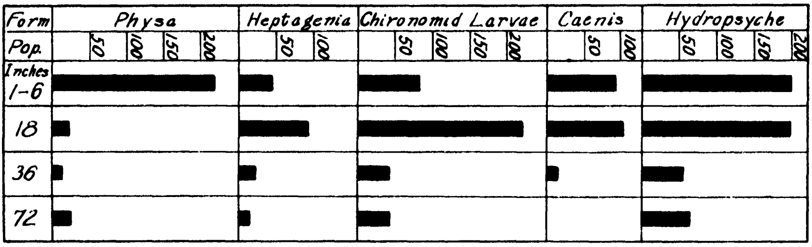

FIG. 13. Total number of certain forms per square yard at each of the depths studied.

On the other hand, the conditions within the six inch contour would appear to favor efficient respiration, namely, constant water movement and the absence of an accumulation of sediment. Other factors to be considered are the increase in pressure which comes with greater depth and the differences on the part of the animals in their responses to such stimuli as current and light intensity.

SUMMARY

The density of the bottom population and the variety of its forms within the six foot contour of western Lake Erie were found to depend upon the type of the substratum, the character of the vegetation and the depth of the water. Such physical factors as temperature, oxygen, carbon dioxide, and pH were in general so uniform over the area studied that they did not appear to be critical factors. The densest population was in less than thirty-six inches of water. Half of the animals represented occurred in maximum numbers within the six inch contour although, due to great numbers of chironomids, the largest total population was at the eighteen inch contour. Shelving rock shore was the most densely populated because of great numbers of chironomid larvae and *Lymnaea* but rubble shore had the greatest variety of animals present in maximum numbers. The smallest number of forms occurred on sand bottom, the largest variety on rubble. Among the plants, *Scirpus* was most densely populated, again due to great numbers of chironomids, but it also was inhabited by the smallest variety of animals. The predominant group of animals in point of numbers and variety of situations inhabited was that of the chironomid larvae. The foregoing conclusions are based upon studies carried out during several recent summers, particularly during the summers of 1929 and 1930.

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THE RELATION OF SOILS AND FOREST VEGETATION OF THE LAKE STATES REGION

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Morozov, the father of Forest Sociology, said in his text: "the forest growth is under influence of climate, but in a direct relation with the soil. . . ." Climatic factors are responsible in a large scale for the boundaries of distribution of forest species, while the soil determines more precisely the composition of the main forest stand, the occurrence of shrubby and herbaceous vegetation, the intensity of growth, the possibility of natural reproduction, etc.

Soil consists of mineral matter, organic remains, water, air, and living organisms. All of these components are of importance with regard to forest growth, and their influence may be studied in many different ways. For the purpose of a broad correlation of soil and forest growth, however, the analysis of soil may be limited to the following: (1) the consideration of topographic features and the state of underground water; (2) the study of soil texture and structure; (3) the study of geological and genetic peculiarities of the soil profile.

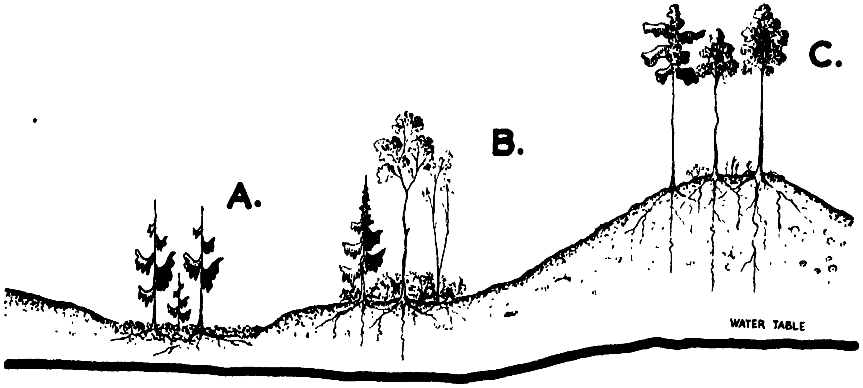

Fig. 1. Relation of forest growth to water table.

According to the classification of Warming, there are three principal types of forest soil as related to underground water; (*A*) Soils in which roots of the plants are permanently under influence of the water table; (*B*) soils in which the roots are periodically under the influence of the water table, either directly or by means of capillarity; and (*C*) soils in which root penetration is entirely above the water table (fig. 1).

(*A*) If a locality is under the influence of underground water continually, a swamp is formed, and the " soil " consists of an accumulation of organic matter or peat. Peat is usually classified on the basis of the composition of organic material into " fibrous peat," " sphagnum peat," " fine woody peat," " coarse woody peat," etc. In case the organic matter is mixed with inorganic matter (silt and clay), the soil is called " muck." The limiting factor of swamp-forest growth is the degree of water stagnation, and all conditions of excessive moisture are usually perfectly correlated with the vegetation.

In the Lake States, particularly, the fibrous peat produces no forest growth, but sedges; sphagnum peat supports pure or mixed stands of black spruce and tamarack; fine woody peat supports water-loving hardwoods—black ash, elm, red maple, yellow birch, willow, and numerous shrubs; coarse woody peat is correlated with white cedar (*Thuja*); the typical vegetation of muck is alder.

(*B*) If, further, a locality is under the partial influence of the water table, the soil consists of poorly drained mineral material, called either " Swampy podsol," or " Glei soil." This type of soil is a transitional form between the swamp and well drained upland soil.

Poorly drained mineral soils of the Lake States Region are characterized by so-called " coniferous-hardwood," or " hardwood-coniferous " types of forest cover. If poorly drained soil is of a sandy nature, the forest stand as a rule consists of white pine, *Pinus strobus,* Norway pine, *P. resinosa,* Jack pine, *P. banksiana,* with a mixture of aspen, paper birch, and sometimes oaks. If poorly drained soil is of a loamy character, the forest stand includes chiefly water-loving hardwoods—ash, elm, red and sugar maple, yellow birch, and an admixture of conifers—white pine, hemlock, spruce, and especially balsam fir.

(*C*) Finally, if the locality is entirely above the influence of the water table, the composition of the forest stand is determined by the texture and in some cases by the structure of the soil.

The texture of the soil is given by the proportion of coarse (gravel and sand) and fine (silt and clay) soil material. The silt and clay portion is largely responsible for the water-holding ability of soil, amount of aeration, and is a chief source of plant nutrients. In a broad way, all well drained soils may be divided into three principal groups: sandy soils, loamy soils, and clay soils. In general, the sandy soils are correlated with the pine species; loamy soils with hardwoods; clayey soils with both hardwoods and conifers.

In a detailed classification, the poorest sands, such as wind-blown sands, have the lowest water-holding capacity, and a minimum of plant food and support primarily Jack pine; the better outwash sands, or " loamy sands," have a greater water-holding capacity, and more available nutrients; Jack pine and Norway pine are here common; the best sands, particularly morainic. sands, or " sandy loams," support Norway pine and white pine. On poor sandy soils pine stands may include an admixture of shrubby oaks (Jack oak, *Quercus ellipsoidalis,* black oak, *Q. velutina*). On better sandy soils, pine stands may include an admixture of light-demanding hardwoods, such as aspen, paper birch, and the better oaks (red oak, *Q. borealis,* and white oak, *Q. alba*). All of these hardwoods, as well as Jack pine, are especially common on cut-over or burned-over areas.

Loamy soils may be separated into two distinctly pronounced types: " silt loams " and " clay loams." Silt loams have a perfect internal drainage and aeration, and support hardwood stands of sugar maple, *Acer saccharum,* basswood, and occasionally an admixture of white pine. Clay loams have poor internal drainage and insufficient aeration, and support the hardwood stands of the maples, elm, and yellow birch, *Betula lutea,* occasionally with admixture of hemlock, and balsam fir.

Clay soils are very peculiar with regard to their relation to the forest growth. On one hand, the large water-holding capacity of clay soils may cause excessive moisture, poor aeration, and other conditions similar to those of poorly drained mineral soils. On the other hand, an enormous absorptive ability of the colloidal clay particles of these soils may result in a minimum availability of water to the plants, and thus may create the condition of so-called " physiological dryness." Finally, in many cases, clay soils are distinguished by a peculiar prismatical structure, which leads to a very satisfactory aeration of the soil. As the result of all these modifications, the clay soils show a very wide range of forest species of both hydric and xeric character: hardwoods, such as sugar and red maple, yellow birch, elm, ash, aspen, white birch, and conifers, such as white spruce, balsam fir, white pine, Norway pine and even Jack pine.

The dependence of forest growth upon the state of underground water, soil texture and structure, internal drainage and aeration, as outlined, represents only one phase of the correlation of soil and forest growth. In many cases this problem is more complex, due to the influence of so-called " genetic " peculiarities of the soil profile, due to the special chemical composition of the soil, and sometimes due to the presence or absence of organic matter.

All the factors affecting forest growth, such as climate, soil moisture, and soil texture, effect at the same time certain chemical and physical changes of the soil. They cause the so-called " soil degradation " or " podsolization." Also, the composition of the forest vegetation itself takes a considerable part in these processes.

As has been proved by the classical work of the American soil scientist, Hilgard, degradation of the soil is dependent first of all upon the state of precipitation and temperature.

In the regions of high precipitation and low temperature, there is a surplus of snow and rain water which percolates down into the soil. The percolating water gradually dissolves easily soluble chemical compounds (bases), and leaches them down into the lower part of the soil profile. The impoverishing of the upper soil layer in the electrolites (Ca, Mg) leads to the incomplete decomposition of organic matter, which accumulates as raw humus, or as peat material. This is associated with formation of organic acids, and with the concentration of large quantities of free hydrogen ions in the so-called organic absorptive complex. The presence of H ions affects the larger solubility of the humus and its intensive leaching in the form of colloids. The colloidal solution of the humic part of the soil posseses a considerable physical and chemical energy, is very movable, and is well adapted for the development of the microorganisms. All these peculiarities make the colloids of humus the most active factor of soil degradation, and under their influence follows the dissolving of the iron and aluminum sequi-oxides. The percolating water leaches these compounds down into the lower parts of the soil, where the solution comes in contact with bases, and is precipitated. Such a translocation of Fe and Al leads to a discoloration of the upper " podsolic " or eluvial soil layer, and to an intensive rusty color of the lower " accumulative " or illuvial layer.

As a result of the processes of soil podsolization, the upper soil layer may be entirely depleted of mineral plant food. At the same time the chemical compounds in the lower layer of the soil may accumulate in a form unavailable to the plants.

Aside from the climatic influences, the degradation of forest soil to a large extent depends upon the topography, amount of silt and clay particles, content of lime, and occurrence of either coniferous or hardwood species. With regard to the amount of percolating water, soils are more leached or podsolized in depressed areas than in areas having convex relief. Coniferous species, with their acid forest litter, increase podsolization, while the hardwood species, containing in the forest litter a considerable amount of bases, retard podsolization. The absence of silt and especially of clay particles moderates podsolization; in pure sandy soils, water percolates into the soil with great speed and has not sufficient time for dissolving and leaching of iron, aluminum and other compounds. Also, the mineralization of forest litter on sandy soils is nearly always complete, and no strong organic acids are formed. If sandy soil contains a large amount of clay, the worst type of podsolization may be observed. Clay particles leach down and cause a cementation in the lower soil layer, and in this way form a stone-like " hardpan " or " ortstein " layer. The presence of silt in soil moderates the hardness of an ortstein layer. Good forest loams, with a large amount of silt material, never show, therefore, " cemented " horizons. A large amount of clay in the silty soil, however, may effect a " compactation " or " stickiness " of the illuvial soil layer, which causes poor " internal drainage," *i.e.*, a permanent saturation of soil with water, and insufficient aeration. Under such a condition, processes of reduction take place and the soil shows a peculiar " rusty " mottling of iron oxides. In this way podsolization creates poorly drained soils in upland relief, far above the real water table.

Presence of lime or other carbonates in soil material retards podsolization more than anything else. Soils forming upon carbonaceous substratum, or the so-called "Rendzinas," in the earlier stage of development have so much basic material, and such a high alkali reaction, that forest vegetation cannot grow upon them. Therefore, unleached soils, with carbonaceous substratum, or rendzinas, are usually occupied by prairie vegetation, and in this country are called "Prairie soils." Over a long period of time prairie soils located in the podsolic region are gradually degraded by the permanent percolating of water. They lose humus, soluble bases, and high reaction in the upper layer. As a result of this degradation, forests occupy the area, and from rendzina is formed "Forest soil of carbonaceous substratum," also called "gray-brown forest soil." Under the forest cover the process of leaching becomes greater, and "degraded rendzina" becomes gradually a normal forest soil, *i.e.*, "Podsolic soil."

All of these modifications of parent soil material, as outlined, may be summarized in the following scheme into several genetic soil types:

SOILS OF NON-CARBONACEOUS SUBSTRATUM

1. UNDEGRADED or SLIGHTLY PODSOLIZED SOILS ("Sandy barrens" and "Mull loams")
2. PODSOLIC SOILS (leached out forest soils)
3. PODSOLS (strongly leached, sometimes cemented or compacted forest soils)
4. SWAMPY PODSOLS or GLEI SOILS (Poorly drained mineral soils, "Swamp border soils")
5. SWAMPS (Organic soils: peat and muck)

SOILS OF CARBONACEOUS SUBSTRATUM

6. HUMUS—CARBONACEOUS SOILS ("Prairie soils," "Rendzina")
7. FOREST SOILS OF CARBONACEOUS SUBSTRATUM (Degraded rendzina, "Gray-brown forest soils")

Podsolization has a tremendous influence upon both soil and forest growth. First of all, podsolization entirely modifies the texture of soil. The accumulation in the illuvial layer of clay and colloidal particles considerably increases the water-holding capacity, and in this way sandy soil may be converted ecologically into sandy loam, or even a heavier soil. This influence of podsolization is especially pronounced in the case of ortstein formation. The ortstein horizon often has an enormous water-holding capacity and may create the condition similar to that of poorly drained mineral soils. For this reason, the classification of soil on the basis of texture is reliable only when the genetical features of the soil profile are considered.

As to forest growth, a slight podsolization of sandy soils, always associated with the presence of some fine soil material and larger moisture, increases the productivity of pine stands. Considerable podsolization of sandy soils, associated with the cementation of the lower soil layer, also increases the moisture content, and makes it possible for a larger number of forest species to grow (white pine, hemlock, aspen, birch, etc.). However, at the same time, the cementation of soil has a number of unfavorable influences upon forest growth. It may cause excessive moisture in the spring, or a breaking off of capillary water and drought in the summer. It may effect an unsatisfactory reproduction, due to impoverishing of the eluvial layer, and imperviousness of illuvial layer. Finally, the cementation may cause a windthrow of the forest stand.

Podsolization of non-calcareous loamy soils has somewhat similar effect upon the forest growth. The best growth and natural reproduction of sugar maple and other hardwoods are found on the undegraded " mull-loams." A strong podsolization of loams, resulting in the formation of a sticky, mottled horizon brings, as a rule, an admixture of yellow birch and hemlock, and leads to poor growth of the sugar maple, which shows in advanced age the so-called " dry tops."

Podsolization has the most favorable influence upon forest growth in cases of soils having carbonaceous parent material. Under such a condition, progressive leaching acts as a weapon for the forest in its struggle with the prairie, influences the distribution of forest vegetation and stimulates the growth of forest stands.

All of the cases mentioned above find an excellent illustration in the territory of the Lake States. The northern portion of this region is distinguished by a non-calcareous or non-carbonaceous substratum, and by the occurrence of different types of podsolic soils and swamps. The southern portion includes considerable areas having carbonaceous material (glacial limey deposits, residual limestone and dolomite) and is characterized by the occurrence of prairie soils and gray-brown forest soils.

Taking into consideration the genetical peculiarities of the soil profile, the broad correlation of soils and forest species of the Lake States region appears as the following soil-forest associations (figs. 2, 3):

I. CARBONACEOUS SOILS

1. Humus-carbonaceous soils (Prairie soils; Rendzinas)	Grass vegetation "Prairie type" (natural boundary of forest distribution).
2. Forest soils with carbonaceous substratum (Gray-brown forest soils)	Oak, hickory, walnut, butternut.[1] "Oak-hickory type."

II. UNDEGRADED OR SLIGHTLY PODSOLIZED SOILS

1. Sandy soils	White pine, Norway pine, Jack pine and scrub oak. Different "Pine types," and "Jack pine-scrub oak type."
2. Loamy soils	Sugar maple, oak, beech, basswood, elm, white pine. "Hardwood type" or "Hardwood-white pine type."

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[1] This includes only the most typical species on the soils outlined.

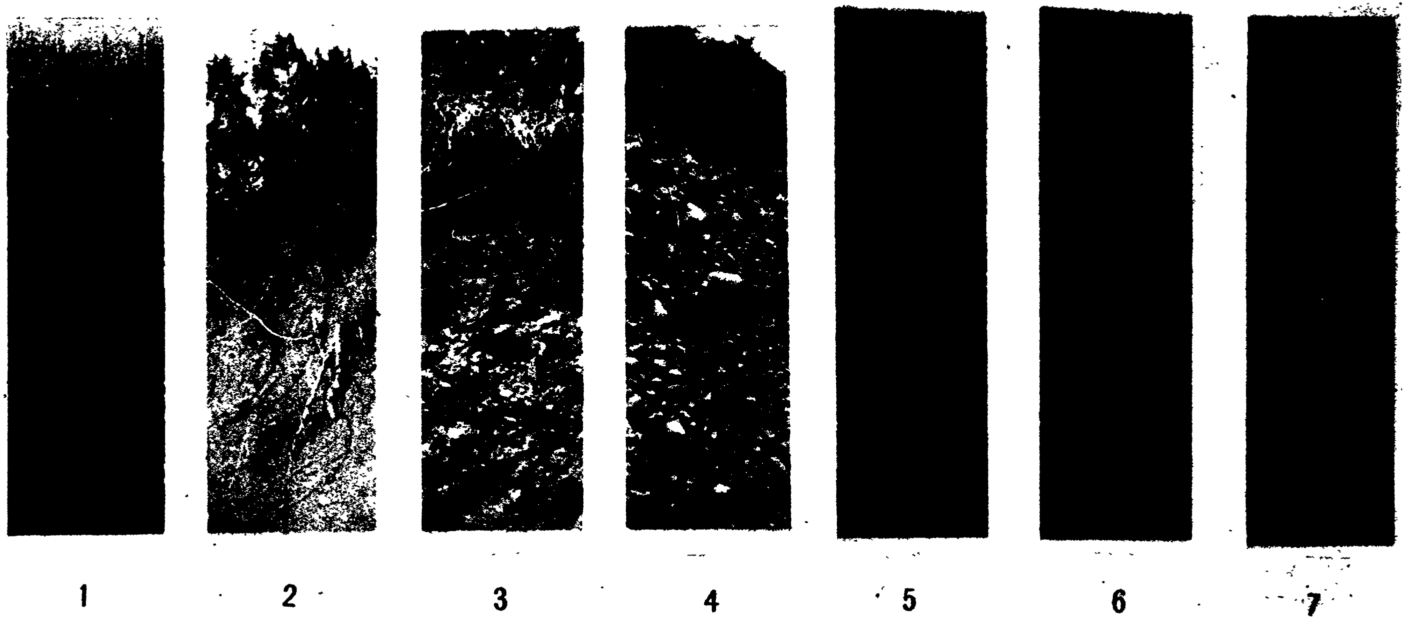

Fig. 2. Typical profiles of sandy soils. 1. Prairie sand; humic sand with carbonaceous substratum. 2, 3, and 4, Undegraded sands: 2. Wind-blown sand; 3. Outwash loamy sand; 4. Morainic sandy loam. 5 and 6. Podsolic sands: 5. Podsolic outwash loamy sand; 6. Sandy loam podsol with Ortstein layer. 7. Poorly drained sand; alluvial sand with muck layer.

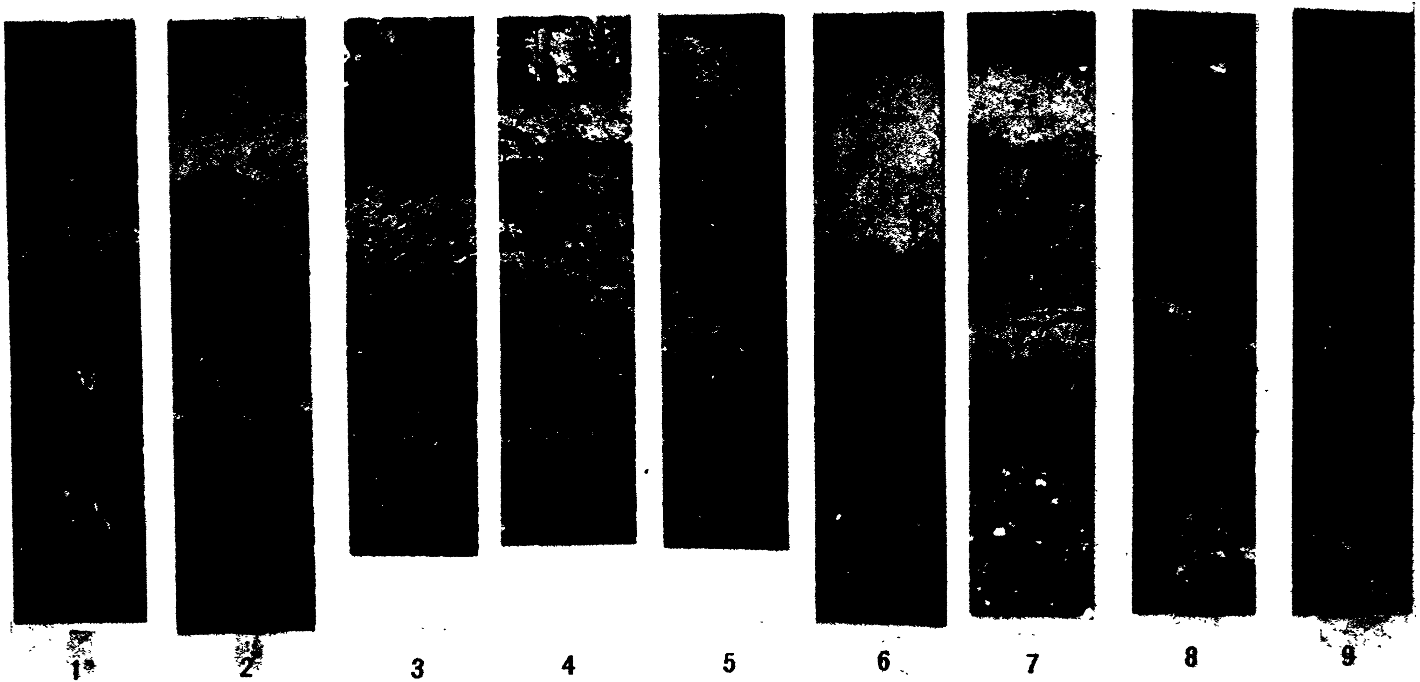

FIG. 3. Typical profiles of heavy and organic soils. 1. Prairie soil or rendzina; humic loam with carbonaceous substratum; 2. Grey-brown forest soil; degraded calcareous silt loam with structured subsoil. 3, 4, and 5. Slightly podsolized soils, or mull-soils: 3. Lacustrine clay; 4. Morainic silt loam; 5. Morainic loam. 6. Podsol; morainic fine sandy loam with ortstein layer. 7. Swampy podsol; morainic loam with glei layer. 8 and 9. Organic soils: 8. Muck; 9. Peat.

III. Podsols, Ortstein Podsols

1. Sandy soils	White pine or hemlock. "White pine type" or "Hemlock type."
2. Loamy soils	Hemlock, yellow birch, sugar maple. "Hardwood-hemlock type."

IV. Swampy Podsols, Glei Soils

1. Sandy soils	White pine, Norway pine, Jack pine, hemlock, aspen, paper birch, oak, etc. "Coniferous-hardwood type."
2. Loamy soils	Red maple, sugar maple, elm, ash, yellow birch, hemlock, balsam fir, white spruce. "Hardwood-coniferous type."

V. Organic Soils

1. Muck	Alder. "Alder type."
2. Fine woody peat	Black ash, elm, red maple, birch, willow, balsam fir. "Hardwood-swamp type."
3. Coarse woody peat	White cedar, spruce, balsam fir. "Cedar-swamp type."
4. Sphagnum peat	Black spruce, tamarack. "Coniferous-swamp type."
5. Fibrous peat	Swamp grass vegetation. "Marsh type." (Natural boundary of forest distribution.)

Many of the soil and forest types of the Lake States Region are distinguished by characteristic ground cover vegetation and shrubs (fig. 4).

The poorest, almost unproductive, wind-blown sands are characterized by the occurrence of xerophytic mosses and of lichens of the genus *Cladonia*, particularly *C. rangiferina*. Outwash sands are associated with New Jersey tea, *Ceanothus americanus;* bearberry, *Arcostaphylos uva-ursi;* low blueberry, *Vaccinium pennsylvanicum*. The most typical plants of morainic sands are sweet fern, *Myrica asplenifolia*, and wintergreen, *Gaultheria procumbens*. The better outwash and morainic sands, as well as podsolic sands, contain fairly well developed growth of hazel, *Corylus americana;* aromatic wintergreen, *Gaultheria procumbens;* shin leaf, *Pyrola* spp.; trailing arbutus, *Epigaea repens;* blueberries, *Vaccinium pennsylvanicum* and *V. canadensis;* bracken fern, *Pteris aquilina;* and wild lily-of-the-valley, *Maianthemum canadense*. The species last mentioned occurs in the most podsolized spots. The strongly podsolic phase of heavier sandy soils shows a number of typical raw-humus plants of a saprophytic nature, such as ground hemlock, *Taxus canadensis, Clintonia borealis, Maianthemum canadense, Cornus canadensis, Mitchella repens, Linnaea borealis* and *Lycopodium* spp.

Well drained loams usually contain a rich association of herbaceous plants, mainly maidenhair fern, *Adiantum pedatum;* sweet Cicely, *Osmorhiza clay-*

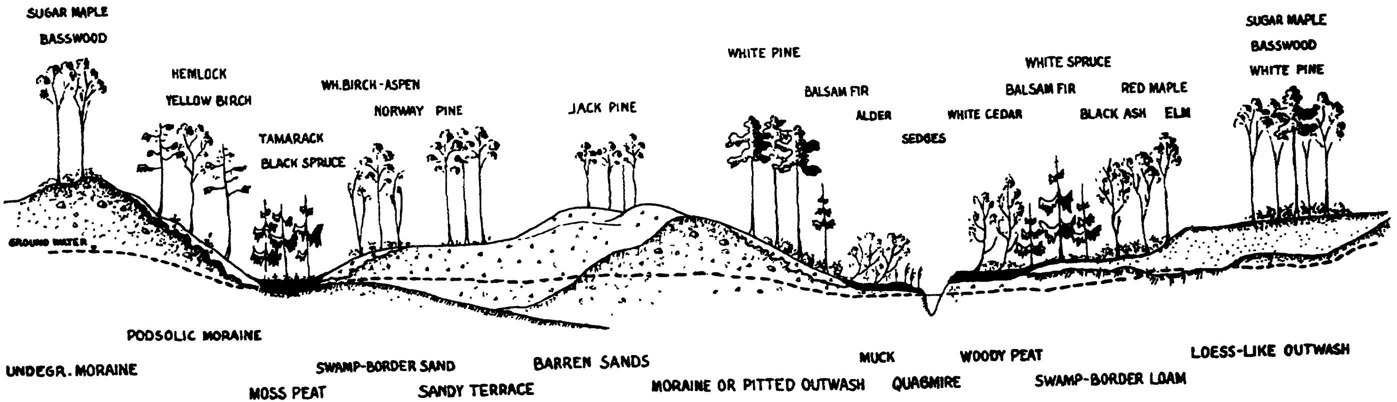

Fig. 4. General scheme of the original distribution of forest species in relation to the water table, texture of the soil and podsolization in the glaciated area of the podsol region of the lake states.

toni; meadow rue, *Thalictrum dioicum;* wild sarsaparilla, *Aralia nudicaulis;* waterleaf, *Hydrophyllum* spp.; hog peanut, *Amphicarpa monoica;* vetchling, *Lathyrus ochroleucus; Trillium* spp.; Solomon's seal, *Polygonatum biflorum;* false Solomon's seal, *Smilacina racemosa;* twisted stalk, *Streptopus roseus;* bellwort, *Uvularia perfoliata;* dogbane, *Apocynum; Smilax* spp., etc. Heavy loams with mottled subsoil support many of the plants mentioned above, but are characterized by a growth of ferns, such as *Phegopteris polypodioides, P. dryopteris, Pteris aquilina, Onoclea struthiopteris, O. sensibilis, Aspidium spinulosum* var. *intermedium, Asplenium filix-femina,* and *Osmunda cinnamomea;* the occurrence of largeleaf aster, *Aster macrophyllum;* Jack-in-the-pulpit, *Arisaema triphyllum, Clintonia, Maianthemum, Equisetum, Trientalis,* etc.

The most typical ground vegetation of poorly drained mineral soils is the bunchberry, *Cornus canadensis,* ferns, and mosses such as *Polytrichum, Hylocomium, Mnium, Leucobryum,* and *Sphagnum.* A number of raw-humus plants such as *Clintonia, Maianthemum, Lycopodium* are also common here. Ferns prevail on poorly drained heavy soils, especially with " mucky " horizon, while bunchberry occurs rather more on the poorly drained sandy soils, and is particularly common in the so-called " Swamp-border type."

Lacustrine clays with a fair drainage and aeration have the ground flora somewhat similar to that of sandy soils; the characteristic plants are species of *Anemone, Fragaria,* and *Trifolium.* Poorly drained or strongly podsolized lacustrine clays are characterized by the presence of water-loving and saprophyte-like species, such as dwarf raspberry, *Rubus* spp., *Gallium, Equisetum, Cornus, Clintonia, Lycopodium,* etc.

Poorly drained organic soils show several well pronounced associations. Muck (clayey peat) and fine woody peat (hardwood swamp) are characterized by numerous shrubs, such as tag alder, *Alnus;* willow, *Salix;* gooseberry, black currant, *Ribes* spp.; witch-hazel, *Hamamelis virginiana;* dwarf raspberry, *Rubus;* dogwood, *Cornus alternifolia;* among the herbaceous plants are common nettles, *Urtica,* and *Laportea;* bedstraw, *Gallium;* tall meadow rue, *Thalictrum;* ferns, species of *Carex, Marchantia polymorpha,* and mosses. Coarse woody peat (Cedar swamp), is correlated with sorrel, *Oxalis* sp., *Maianthemum,* goldthread, *Coptis trifolia,* bunchberry, *Cornus canadensis, Clintonia borealis,* creeping snowberry, *Chiogenes hispidula,* miterwort, *Mitella nuda,* etc. Sphagnum peat usually has one of the most typical associations of the plant kingdom; the most important members of this being: species of sphagnum (*S. tenellum, S. capillaceum, S. fuscum,* etc.), *Polytrichum* and other mosses, leatherleaf, *Chamaedaphne calyculata;* Labrador tea, *Ledum groenlandicum;* American cranberry, *Vaccinium macrocarpon;* twin flower, *Linnaea borealis;* laurel, *Kalmia;* bog rosemary, *Andromeda;* pitcher plant, *Sarracenia;* blueberry, *Vaccinium;* aromatic wintergreen, *Gaul-*

theria procumbens, and a number of xeromorphic plants such as wintergreen, sweet fern and reindeer moss. Fibrous peat is confined to the species of sedges, club rush, *Scirpus;* bog rush, *Juncus;* cotton grass, *Eriophorum;* cattail, *Typha,* and other swamp plants.

The writer is indebted to Professor A. R. Whitson, Chairman of the Department of Soils, University of Wisconsin, for the final revision of the manuscript and for helpful suggestions, and to H. F. Scholz, Lake States Forest Experiment Station, for several of the photographs of soil profiles.

STUDIES IN MASS PHYSIOLOGY: THE EFFECT OF NUMBERS UPON THE OXYGEN CONSUMPTION OF FISHES[1]

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INTRODUCTION

The study of animal aggregations during the past few years in this and other laboratories has uncovered a large group of interesting and valuable facts concerning the reactions and relations of animals when placed with others of their kind. This body of data has recently been reviewed by Allee ('31). Evidences of a "group effect" have been based upon such things as growth, reproductive rates, survival under toxic conditions, and other similar indices. In the fishes there has been some work on the effects and causes of aggregations. Church ('27) has shown that the growth of certain tropical fishes is conditioned to a considerable extent by the number of individuals present in the aquaria. The retardation of growth when larger numbers were present was ascribed to the presence of accumulated excretory products. Other workers have come to the same conclusions concerning the effects on growth produced by crowding of fishes (Willer and Schnigenberg, '27; Kawajiri, '28).

Much of the work on fish aggregations has dealt with species which ordinarily form schools in nature. Such aggregations seem distinctly different from the vast majority of fishes which do not appear to have the "schooling instinct." An interesting problem presents itself in bridging the gap between the solitary forms and those which exhibit highly integrated mechanisms of aggregation. It was thought probable that even in fishes which show no schooling reactions but which tolerate the nearby presence of other fishes there may be some measurable physiological effect of grouping or crowding other than the effects of growth, knowledge of which would open the way to further investigations upon the general problem of aggregations. Such effects have already been reported. Welty ('30) has shown that in goldfishes, which have not been considered as social, there are differences in learning behavior according to whether the fishes are single or in groups. Thus, it may be that even in animals which have hitherto been thought of as non-schooling, or non-social, there are influences producing effects which have so far been either overlooked or neglected.

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[1] The writer wishes to express his appreciation to Professor W. C. Allee of the University of Chicago for the many helpful suggestions given during the course of this work.

It is the purpose of this paper to examine the respiratory behavior of certain fishes which exhibit little or no schooling tendency in order to determine to what extent a " group effect " is present.

MATERIALS AND METHODS

For this work four genera of fishes were employed. The guppy, *Lebistes reticulatus* Peters, the common mudminnow, *Umbra limi* Kirtland, the goldfish, *Carassius auratus* Linne, and the Atlantic killifish, *Fundulus heteroclitus* Linne served as test animals, and essentially similar results have been obtained in each case. The work was started with the mudminnows, but because of the unavailability of these in certain parts of the year it was necessary to resort to the others.

The oxygen consumption was determined by the Winkler method, Birge and Juday's modification ('11) being used in all cases. Objections to this method, especially as applied to studies of this sort (Heilbrunn, '15) center about the fact that a certain amount of free iodine is removed from the samples by fixation or adsorption because of the presence of slime or of excretory products of the test animals. The seriousness of this defect in the method was tested in the following manner:[2] Four fishes were placed in an open Erlenmeyer flask in one liter of water and left for thirty hours. Samples were taken from this water and iodine of a known strength added. Titrations were made with sodium thiosulfate and the available iodine recovered. The results thus obtained were checked with similar experiments on pure water under identical circumstances. It was found that in the thirty hours enough material was produced by the four fishes to remove the equivalent of 0.00209 cc. of oxygen from the samples. This period of thirty hours is over three times as long as any of the experimental periods, and hence the amount of slime will be in excess of that produced in the experiments. In the running water experiments to be described later the amount of iodine removed by adsorption is even smaller. Since only a negligible amount of iodine is adsorbed in thirty hours, and as the experiments were of a much shorter duration, the amount of removed iodine cannot be regarded as of significance.

Three different methods of experimentation were used which yielded essentially similar results. In all cases Whitman Laboratory well water was used. This was collected in a large carboy and aerated with air for some time before use. It was transferred from the carboy directly to the respiratory chambers. In the case of the running water experiments to be described later, a constant stream of this water was supplied to the respiratory chambers during the course of the experiment. The methods used were as follows:

1. Determination of the oxygen concentration in the medium before and after an experiment with the container stoppered to avoid air contamination during the time of experimentation. This method has been criticised, espe-

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[2] The cooperation of Mr. R. B. Oesting in these chemical analyses is gratefully acknowledged.

cially when the period of time over which the experiment is run is rather long, because of the complications involved when carbon dioxide and other products of metabolism collect in the medium in which the test animals are living, and also because of the reduction of available oxygen as time goes on. In the present work one and two hour intervals were used, but even here there is the possibility of contamination with excretory products having influenced the oxygen consumption.

2. Determination of the oxygen concentration at intervals during an experiment, samples being siphoned from beneath a deep layer of paraffin oil from time to time for analysis. In this method the same criticisms apply as in the first case.

3. The maintenance of a steady rate of fresh water flowing over the fishes during the experiment, collecting samples from time to time and comparing with control samples. The apparatus used was somewhat modified from a setup employed by Keys ('30) in his studies on fish respiration, which it resembled in essentials. In this type of experiment the possibility of contamination by excretory products is at a minimum, but even here there is a chance for some effect from such a substance as carbon dioxide. The rate of flow must be slow enough to measure the amount of oxygen removed by the isolated fishes, and at the same time fast enough to maintain a supply of fresh water to the respiratory chambers, so that the diminished oxygen will not enter as a possible factor. The chambers used held 650 cc. and water passed through at rates varying from 1225 cc. per hour to 1425 cc. per hour.

It is very difficult to analyze with exactness the mass physiology of animals. The relationships which exist between volume of medium, the available space per organism, the effects of various environmental factors (oxygen concentration, excretory products, etc.) are so intricate that usually more than one variable is introduced. In this study eight fishes were used for every experiment. Four of these were grouped into one respiration chamber, and the other four separated into different chambers under conditions as identical with the group as possible. It is recognized that in this system the group occupies the same amount of medium as a single fish, but if space is allowed in proportion to numbers, then one element of crowding or aggregation is lost. In this study, then, unless otherwise specifically stated, a group of four fishes is compared with four isolated individuals and all the containers are treated as much alike as possible. Adequate controls were maintained in each case.

In most of the work on fish respiration the fishes are weighed and the oxygen concentration determined, after which some relation is established between the number of grams of fish and the amount of oxygen removed from the water. In the present work, however, because of the number of fishes used, it was judged better to measure the length of the fishes used and to use the same length throughout. Accordingly, for example, goldfishes with a similar history which measured from 4.00 to 4.20 cm. from the tip of the nose to the base of the tail were selected for use. The mean length in centimeters was 4.10 with a standard error of ± 0.025. As a check on the variability of this length of fish as to weight, ten goldfishes were weighed. The mean weight in grams was 1.800 with a standard error of ± 0.065.

RESULTS

This work was started by testing an apparent discrepancy between the observed and expected ratios of oxygen consumption of isolated and grouped mudminnows. Four fishes were placed in an Erlenmeyer flask having a capacity of 1150 cc. and after the bottle was filled with water, stoppered, care being taken that no bubbles remained, it was allowed to stand for two hours and the amount of oxygen determined. The oxygen consumption of a group of four fishes was compared to that of four isolated fishes treated in a similar manner. Adequate controls were run in each case. All things being equal it is logical to expect that the group of four will consume approximately four times the amount of oxygen that a single fish uses, or approximately the same as that used by four comparable, but isolated, fishes. A consistent difference, however, soon led to the conclusion that some factor was modifying the oxygen consumption of the group (assuming that the consumption of an isolated individual is normal). The results of twelve experiments are shown in table I.

TABLE I. *Total amount of oxygen consumed by four isolated and four grouped mudminnows over a period of two hours. The temperature was practically constant (25°–26°)*

	Grouped		Isolated		
Control O_2 tension at end of experiment in cc. per liter	O_2 tension at end of experiment in cc. per liter	O_2 consumed in cc.	Mean O_2 tension at end of experiment in cc. per liter	O_2 consumed in cc.	Difference in cc.
6.49	6.02	0.54	6.25	1.10	0.56
6.39	6.04	0.40	6.06	1.52	1.12
6.69	5.97	0.83	6.21	2.20	1.37
6.26	5.80	0.53	6.00	1.20	0.67
6.56	6.08	0.55	6.40	0.74	0.19
6.45	5.95	0.57	6.34	0.51	−0.06
6.52	6.10	0.48	6.27	1.15	0.67
6.39	5.65	0.85	6.21	0.83	−0.02
6.55	6.05	0.57	6.31	1.10	0.53
6.37	5.92	0.52	6.22	0.69	0.17
6.53	5.62	1.05	6.26	1.24	0.19
6.65	5.96	0.79	6.37	1.29	0.50
Mean 6.49±.03	5.93±.04	0.64±.05	6.24±.03	1.13±.12	0.49±.12

The figures in the columns of oxygen consumed refer to the total consumption of oxygen. This can be measured directly for the grouped fishes. For the isolated fishes it is necessary to summate the oxygen consumption of four different fishes to obtain the value. In both columns the values have been corrected to account for the actual size of the container, so that the figure in each case represents the actual amount of oxygen consumed. These data indicate that at no time did the oxygen tension of the medium become lower than 5.62 cc. per liter for the group and 6.00 cc. per liter for the isolated fishes. Certainly at these tensions the decreased oxygen supply could not have been responsible for the lower oxygen consumption per fish for the group. The mean oxygen consumption for the four isolated fishes was 1.08 cc. while for the four in the group it was 0.64 cc. Considered statistically according to the method of Student ('25) these data have a value of 0.004, a figure which is well above the threshold of significance. Only two cases gave evidence that the total oxygen consumption of the isolated fishes was less than that of the group, and these were so small in comparison to the greater differences in the other direction that they have little effect on the general trend.

Experiments of this kind were repeated, using the guppy, and essentially similar results noted. The guppies, because of their smaller size (3.00–3.20 cm.) necessitated a longer time in the medium, and as a consequence, the experiments were allowed to run twelve hours. Table II outlines the results of one experiment of this type, and table III shows the summary of twenty-nine such experiments.

TABLE II. *Effect of numbers present upon the oxygen consumption of the guppy. This experiment was conducted in a manner similar to those summarized in table I, except that a period of twelve hours was used. Temperature 20° C.*

Fishes	O_2 present at end of experiment in cc.	O_2 consumed in cc.	O_2 consumed per fish in cc.
4	5.19	1.48	0.37
1	5.67	1.00	0.96
1	5.70	0.97	
1	5.75	0.92	
1	5.72	0.95	
0	6.67	—	

From table II it can be seen that instead of amounting to about four times the consumption of an isolated fish, under these conditions the group consumption was hardly more than that of a single individual. Table III shows the consistency of the results over a large number of experiments. At no time did the oxygen content of the medium become so low as to be a limiting factor. The lowest value of oxygen concentration in the grouped fishes was 2.30 cc. per liter, which is far above the asphyxial level, and in the isolated fishes the lowest oxygen concentration was found to be 3.84 cc. per liter. At these levels it is safe to assume that oxygen tension does not interfere with respiration. The significance, determined by Student's method, was found to be 0.0000.

The type of work in which the samples are taken at intervals during an

TABLE III. *Summarizing the results of twenty-nine experiments on the guppy. The procedure in the individual experiments was similar to that outlined under table I. Temperature 20° C.*

O_2 tension at end in cc.	Average O_2 consumption of a group of 4 fishes in cc.	O_2 tension at end in cc.	Average O_2 consumption of 4 fishes isolated in cc.	Difference
5.12	0.39	5.52	0.99	0.60
3.39	0.54	4.68	0.71	0.17
5.19	0.37	5.67	0.96	0.59
5.23	0.36	5.52	0.92	0.56
4.73	0.29	5.44	0.44	0.15
5.53	0.12	5.31	0.32	0.20
4.85	0.27	5.46	0.46	0.19
4.82	0.28	5.37	0.41	0.13
5.46	0.09	5.53	0.36	0.27
5.42	0.14	5.58	0.27	0.13
5.17	0.21	5.59	0.37	0.16
5.38	0.23	5.81	0.35	0.12
5.20	0.27	5.73	0.40	0.13
5.31	0.25	5.71	0.49	0.24
4.43	0.29	4.68	0.72	0.43
4.89	0.26	5.33	0.47	0.21
5.24	0.17	5.45	0.34	0.17
4.60	0.52	5.99	0.48	−0.04
4.08	0.24	4.95	0.64	0.40
2.30	0.76	3.94	1.05	0.29
4.70	0.33	5.24	0.44	0.11
4.75	0.21	4.86	0.54	0.33
4.89	0.22	5.00	0.66	0.44
3.29	0.34	3.84	0.60	0.26
5.24	0.14	5.11	0.33	0.19
2.92	0.59	4.32	0.63	0.04
5.13	0.35	5.80	0.43	0.08
5.22	0.14	5.34	0.44	0.30
4.85	0.27	5.46	0.46	0.19
Mean 4.74±.14	.30±.01	5.25±.10	0.54±.04	.24±.03

experiment is illustrated by the work on the common goldfish, a hardy form, and one much used in laboratory work. A group of four fishes was placed in an Erlenmeyer flask, and was covered with three or four centimeters of a heavy paraffin oil, which was found to be quite effective in isolating the medium from the atmosphere, at least in the interval used. The group of four fishes was compared from time to time with four isolated fishes under similar circumstances. An oil covered blank was run simultaneously in order to check on the original concentration, and on the effectiveness of the oil in maintaining a block.

As stated above, this method also allows an opportunity for the action of carbon dioxide and other products of metabolism that may accumulate as the time progresses, and for a gradual decrease in the oxygen concentration of the medium. Experiments of this type are of value, however, because the comparison of groups and isolated individuals has been the major point of interest, and any effect of crowding will only serve to bring out more effectively the difference which exists between fishes under these different conditions.

Twelve experiments were performed, ten with the volume of 2175 cc. and two with the volume of 1150 cc. In both of these cases the same principles are illustrated, the only difference appears to be a somewhat quicker diminution of the oxygen supply in the smaller volume. Table IV and figure 1 show the results of ten experiments with goldfishes in the two liter volumes. In figure 1 the average oxygen consumption per fish from the beginning of the experiment is shown in hourly intervals over a period of nine hours. It is apparent that fish for fish the amount of oxygen consumed is much less in the members of the group than in the isolated individuals. The significance in all cases is far above the threshold as determined by Student's method.

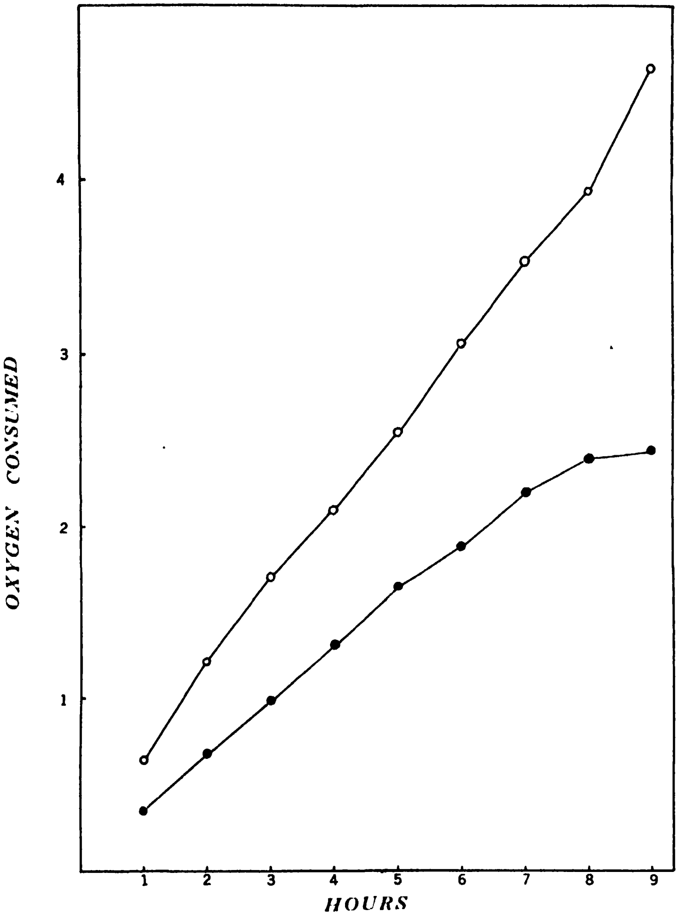

FIG. 1. Difference between grouped and isolated fishes over a period of nine hours. These results are in cc. oxygen consumed. ○ = isolated. ● = grouped.

An examination of the curves in figure 1 will also reveal that the rates of oxygen consumption appear to be quite constant. The only exception to this

TABLE IV. *Mean total amount of oxygen consumed in cc. hour by hour by grouped and isolated goldfishes. This table is based upon ten experiments. Standard errors are shown. Temperature 26°–27° C.*

Hour	Group of 4 fishes	4 Isolated fishes
1	0.362±0.029	0.642±0.032
2	0.686±0.045	1.225±0.053
3	0.996±0.051	1.705±0.066
4	1.311±0.070	2.112±0.107
5	1.647±0.077	2.551±0.153
6	1.881±0.079	3.038±0.150
7	2.209±0.052	3.564±0.163
8	2.405±0.047	3.945±0.154
9	2.450±0.011	4.660±0.095

seems to be the termination of the group curve, which flattens out perceptibly after the seventh hour. Up to this time, however, there is no particular irregularity in the rate of oxygen consumption. Under these experimental conditions it is admitted that excretory products are accumulating, and that the oxygen supply is constantly being reduced. If such a product as carbon dioxide, however, is responsible for this phenomenon, then its effect should be shown before the seventh hour, since it is being produced from the beginning of the experiment. The constancy of oxygen consumption during most of the experiment indicates that the changes produced by the fish or fishes living in this restricted experimental volume which includes the accumulation of carbon dioxide and the decreased oxygen are not limiting factors during the early hours of the experiment.

Figure 2 is designed to show the relation between the total consumption of oxygen in groups and isolated individuals and the oxygen tension of the medium. As mentioned above, the respective rates of consumption are quite constant down to near the level of asphyxia, where the consumption is reduced near the seventh hour. Thereafter the consumption difference between the grouped and isolated fishes grows progressively larger on account of the decreased rate of consumption by the grouped fishes. Such differences are without question of significance.

A somewhat more convincing type of experiment is shown in fig. 3 where the groups and isolated fishes were alternated. The isolated fishes of one experiment were placed together and used as the grouped fishes of the next. The group, on the other hand, was separated and the members used as isolated fishes. Unfortunately, this was possible in only three cases, since the post-experimental mortality of the group in these long experiments often amounted to as much as fifty per cent of the individuals. In many of the experiments one or more of the grouped fishes would succumb to the effects of the treatment, and in these cases the fishes were removed as soon as their death was ascertained, and the entire experiment terminated at the following hour. Figure 3 indicates that the fishes consume oxygen at a rate that is strongly influenced, and in fact apparently controlled by the number of individuals present.

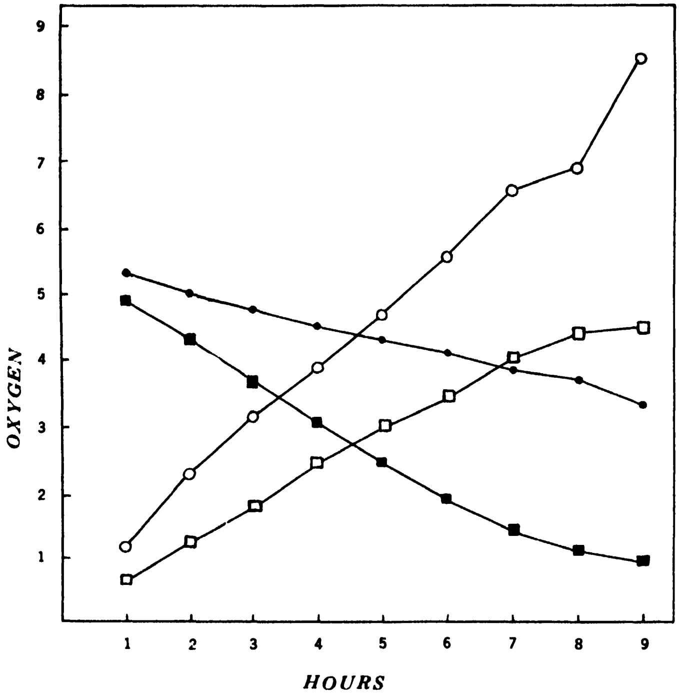

FIG. 2. Relation between the total oxygen consumption in groups and isolated individuals and the oxygen concentration of the medium. ● = Average O_2 tension in cc. per liter of medium of isolated fish. ■ = Average O_2 tension in cc. per liter of medium of grouped fishes. ○ = Average total consumption of four isolated fishes in cc. □ = Average total consumption of four grouped fishes in cc.

The work of Keys ('30) on the respiration of fishes has shown that the best way of measuring the oxygen consumption is to keep running water flowing through the respiratory chambers, thus supplying the fishes with a fresh oxygen supply, and at the same time minimizing the chances for a contamination by excretory products.

An arrangement, similar in principle to that of Keys, was employed and the results obtained as to the relative oxygen consumption of groups and isolated fishes in eight experiments with running water are shown in fig. 4.

The source of water was a large carboy in which Whitman Laboratory well water was aerated and from which it was siphoned to the respiratory chambers. These chambers had a capacity of 650 cc. and the rate of flow was controlled by limiting the outgo by capillary tubes. All chambers were supplied from a common source. The capillary tubes varied somewhat and it was necessary to measure the rate of flow through each one separately. It was found that the rates varied from 1225 cc. per hour to 1425 cc. per hour. Five chambers were run simultaneously, one containing a group of four fishes, and the other four containing one fish each. The entire apparatus was

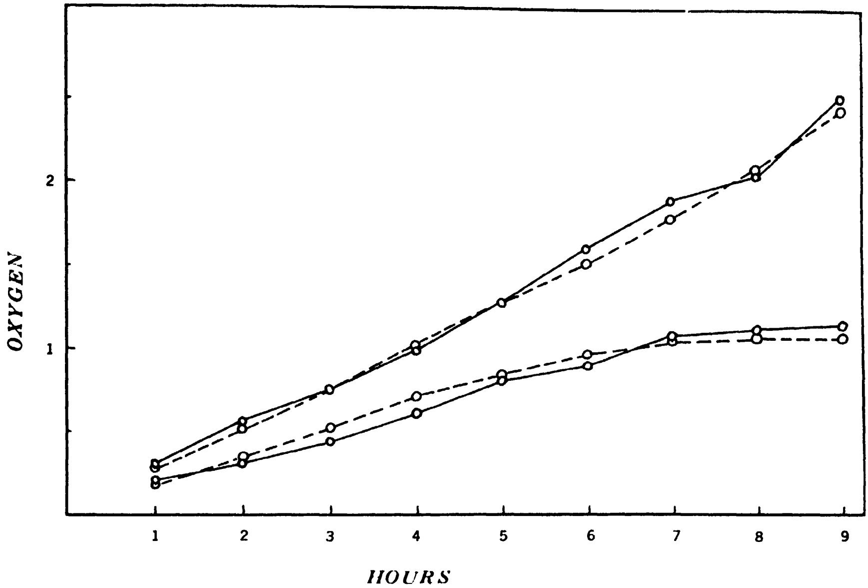

FIG. 3. Results of three experiments in which the isolated and grouped fishes were reversed. Solid lines show the condition before reversal, the upper line representing the consumption of the isolated fishes, the lower line that of the grouped fishes. Dotted lines show the condition after reversal, the upper line representing the isolated fishes and the lower line the grouped fishes.

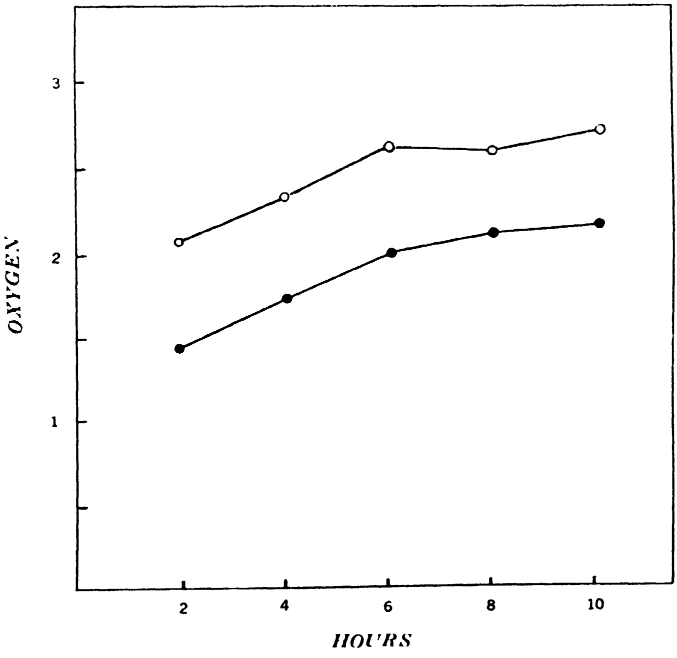

FIG. 4. Difference between grouped and isolated fishes in running water.
● = Group. ○ = Isolated.

immersed in a water bath, and the temperature controlled to any desired point. Samples were drawn from the capillary tubes for analysis. As a check on the oxygen tension of the supply water, samples were drawn from the main siphon line before it reached the respiratory chambers and analyses made. Knowing the oxygen tension before and after the water had passed through the chambers, and knowing the rate of flow, it was possible to calculate the amount consumed by the fishes. At all times the consumption of oxygen in the group was less than the consumption of the isolated fishes. Table V also shows the mean oxygen consumed during these flowing water experiments in cc. per liter, and the significance at two hour intervals over a period of ten hours.

TABLE V. *Difference in oxygen consumption at two hour intervals between four grouped and four isolated goldfishes in running water experiments. Data represent average of eight experiments. Temperature 22° C.*

Hour	Mean O_2 consumed in cc.		Significance of difference[3]
	Group of 4	Isolated	
2	1.44±0.06	2.02±0.11	0.0000
4	1.73±0.13	2.31±0.16	0.0024
6	1.95±0.16	2.66±0.26	0.0040
8	2.07±0.16	2.60±0.25	0.0068
10	2.16±0.34	2.85±0.41	0.0034

[3] 0.01 or less is usually regarded as having statistical significance.

Experiments of this nature were performed upon the Atlantic killifish and similar results noted. The fishes selected were all of the same size and were supplied with flowing sea-water at all times. A measurement of the oxygen tension of the water before and after use by the fishes made it possible to calculate the amount of oxygen removed by the fishes. Table VI shows the oxygen consumed per fish by grouped and isolated animals in eight experiments.

TABLE VI. *Amount of oxygen consumed per fish by grouped and isolated Fundulus under identical conditions. Results in cc. per fish. Temperature 22° C.*

Group of four	Isolated	Difference
0.525	0.822	0.297
0.610	0.877	0.267
0.415	0.747	0.332
0.455	0.781	0.326
0.310	0.816	0.506
0.670	1.167	0.497
0.632	0.738	0.106
0.475	0.886	0.411
Mean 0.512±.040	0.854±.045	0.343±.036

Each of these experiments was performed on a different day, so that the variation which exists between different experiments is not necessarily significant. The conditions under which each individual experiment was run, however, were as constant as possible. The significance of this group of data when tested by Student's method was found to be 0.00007, which is far above the threshold.

Experiments on *Fundulus* also afforded an interesting example of the reversible nature of the "group effect." The oxygen consumption of the fishes was followed over a period of several days, during which time individual fishes were used as isolated forms, as members of a group of two, and as members of a group of four. The amount of oxygen consumed can best be seen by means of figure 5. Thus, it appears that the oxygen consumption of any one fish depends, in part at least, upon the number of individuals present in the respiratory chamber.

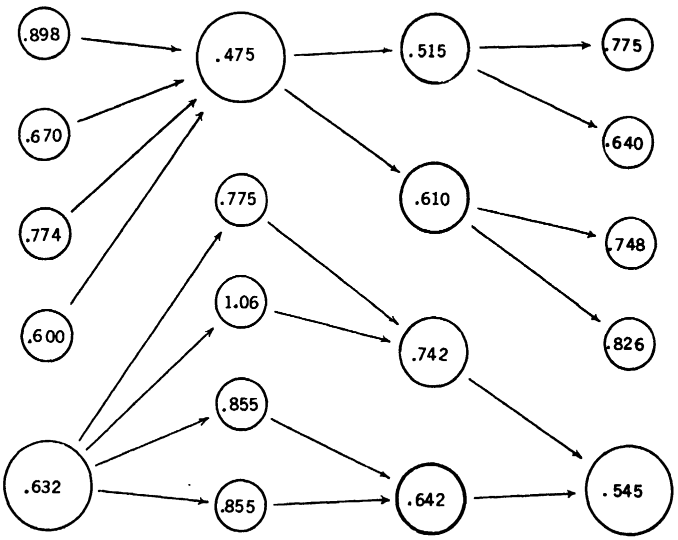

FIG. 5. Change in oxygen consumption of Fundulus according to the number of fishes present. The size of the group is indicated by the size of the circle. Groups of one, two, and four were used, and fishes alternated between these groups. Each column indicates a day. The numbers represent the amount of oxygen consumed in cc. per fish.

The data so far have indicated that a group effect is present when the volume is held constant. By putting fishes into volumes in proportion to the numbers present, however, one element of crowding is lost, and the situation becomes less complex. Such a series of experiments was conducted, and the results shown in table VII. In these experiments a group of four goldfishes was placed in an Erlenmeyer flask which contained two liters of water under the usual thick layer of paraffin oil, and four isolated fishes of the same size were distributed to four half liter flasks in exactly 500 cc. of water under a similar oil layer. Controls were run as before. The data indicate that volume plays a part in controlling the oxygen consumption of the fishes. The "group effect" is lost, and the average consumption of the grouped and isolated fishes is practically equal. By Student's method the significance was found to be 0.2972 which indicates that the difference between the oxygen consumption of the grouped and isolated fishes, although still greater for the latter, is in this case far from being statistically significant.

TABLE VII. *Amount of oxygen consumed in one hour by grouped and isolated goldfishes when the volume of medium is in proportion to the number of individuals present. Temperature 24° C.*

	Grouped		Isolated	
	O_2 tension at end in cc.	O_2 consumed in cc.	O_2 tension at end in cc.	O_2 consumed in cc.
	5.56	0.76	5.46	0.61
	6.96	1.28	6.86	1.35
	5.78	1.48	5.71	1.83
	5.69	0.64	5.47	1.61
	5.34	1.36	5.52	1.19
	5.13	1.12	5.05	1.09
	4.80	1.28	4.86	1.10
	4.55	1.26	4.73	1.06
	4.52	0.96	4.59	1.08
	4.39	0.08	4.05	1.14
	4.97	1.06	4.79	1.31
Mean	5.24±.22	1.03±.11	5.19±.22	1.22±.09

DISCUSSION

Some animals appear to consume oxygen at a rate proportional to the concentration of this gas in their medium, while others are largely independent of the oxygen concentration of the surrounding medium, at least until quite low levels are reached. This whole question has been reviewed at some length by Hyman ('29) so that it seems inadvisable to make a repetition here. An important paper, however, that deserves attention is that of Toryu ('27), which lends considerable weight to the view that fishes are quite independent of the medium tension until the pressure is reduced to the region of 0.2 (vol. per cent), where the consumption begins to fall off. Between 0.2 and 0.75, however, the rate of consumption is very constant. More recently, Keys ('30) on fishes, and Hiestand ('31) on several invertebrates bring the problem up to date with important criticisms of previous work and the applications of more refined methods to the study of respiration. The work of this paper, although not its primary concern, shows that within considerable ranges the oxygen consumption is independent of the oxygen tension of the medium. At lower levels, however, the oxygen consumption falls off. This falling off took place under the conditions of these experiments when the level of oxygen tension was in the region of one cc. per liter.

The aggregational aspect of this question has received little attention in comparison to the great body of data that exists concerning general respiration. Allee ('26) has shown that the rate of oxygen consumption in two genera of land isopods is less with bunched individuals than with isolated animals at the beginning of the experiments. At the end of twenty-four hours, however, this relationship is reversed, and the scattered isopods are consuming oxygen at a slower rate than are the bunched individuals. A similar phenomenon has been shown for the serpent-star, *Ophioderma* (Allee, '27). The grouped forms at the beginning of a starvation period consumed less oxygen than did isolated individuals, but later this relation is reversed, as in the isopods, and the individual serpent-stars had the slower rate of oxygen consumption.

With the fresh water isopod, *Asellus* (Allee, '29) it has been demonstrated that individuals taken from an aggregation in nature consume oxygen at a slower rate than do isopods selected from scattered individuals.

Fowler ('31) shows that significant differences exist between the oxygen consumption of grouped *Daphnia* and that of isolated individuals. The data presented by Fowler appear to show a condition very similar to that of the fishes.

These studies are the only ones known which treat with respiratory differences in grouped and isolated individuals. In the applicable cases cited it was found that during the earlier stages of the experiments grouping was accompanied by a reduction in oxygen consumption. The data presented in this paper show that this is true in certain fishes for at least ten hours. These data appear to be comparable with the first stages of Allee's experiments. They were not continued long enough, and except for the running water experiments, they were not run under the proper conditions to test whether or not a reversal such as he describes would result. Such possibilities remain to be worked out.

It is difficult to account for the difference between group respiration and that of isolated individuals. A number of things at once suggest themselves as possible factors for producing this effect. The factor of reduced oxygen content is the most obvious possibility. This, however, can hardly be said to be of importance since these experiments confirm Toryu's ('27) findings that the oxygen consumption of fishes is quite independent of the oxygen concentration of the medium down to near the asphyxial level. The "group effect" was found to be present at all times. Again, the experiments with running water, in which the oxygen content never approached the asphyxial level, the "group effect" was still prominent. With these facts in mind oxygen tension cannot be regarded as of primary importance.

Excretory products, such as carbon dioxide, may be thought of as having a part in the lowering of the oxygen consumption of the group. Carbon dioxide is produced at all times by the fishes, so that its concentration in the medium grows progressively larger. In view of this it might be expected that the effect of carbon dioxide would reduce the oxygen consumption gradually. This was not found to be true. Well water was used in all the experiments, and the Whitman Laboratory well water is highly buffered with calcium salts. Changes in pH could not be detected by colorimetric methods in the experiments run two hours, and yet the " group effect " is outstanding in these experiments. In the running water experiments, on a basis of the evidence at hand, the more rapid production of carbon dioxide by the grouped fishes cannot be used to account for differences between grouped and isolated fishes.

Activity of some kind might be thought of as a possible factor. Allee ('27), using serpent-stars, was dealing with positively thigmotactic animals, which tended to collect in bunches. The decreased oxygen consumption in the early stages of his experiments has been attributed in part, at least, to " a decreased muscular tonus accompanying the more nearly optimum tactile relations furnished by the bunched condition." With the fishes used in this work, however, there is no such tactile tropic response. The conditions imposed upon the fishes by the Erlenmeyer flasks are not as remote from their natural habitat as are the same conditions for serpent-stars. At least, no difference could be detected between the activity of groups and isolated individuals by the observational method, although no quantitative methods were employed in this determination.

Volume seems to play some part in controlling the oxygen consumption of fishes, since by allowing volume in proportion to the number of individuals present, the " group effect " is lost, and the amount of oxygen consumed by the fishes in the group and the isolated individuals is essentially the same. This fact, while interesting, helps little in explaining the " group effect " when the volume per group and per individual is the same.

Ecological investigations have for years been concerned with the detection and measurement of the effect produced by environment upon the organism. Much of the effort of the ecologist has been devoted to an analysis of the physical aspects of the environment, and to the relationships of individuals or communities to these physical surroundings. Biotic factors, on the other hand, have not, until comparatively recently, received the same attention. It is becoming increasingly clear, however, that delicate and subtle biotic mechanisms are at work within the confines of a restricted environment, and that these produce definite and important changes in the interactions within such a community. As stated in the introduction to the present report, many of these relationships have recently been reviewed by Allee ('31) who found that these biotic effects may be classified according to whether they produce beneficial or harmful results. The biotic effects reported in this paper are not easily incorporated into such a scheme. Whether reduced oxygen consumption among members of a group is harmful or beneficial for the individual depends on the other conditions that are operating. It is evident, however, that the behavior of the individuals of a group is modified in response to the presence of others, and that the modification can be measured by differences in oxygen consumption under conditions when more obvious behavior effects cannot be observed. Such facts must be considered in ecological studies on community organization. The effects noted here have been found in relatively simple communities, but until otherwise demonstrated, it is logical to assume that such effects are also present in the more complex communities in nature.

CONCLUSIONS

1. When four fishes are present in a given volume the amount of oxygen consumed per fish is lower than the amount consumed by an isolated fish in the same volume.

2. This phenomenon has been observed in four genera of non-schooling fishes, and it is suggested that it may be a general rule for all such fishes.

3. The "group effect" is found to be reversible, and the respiration of any individual fish can be altered by increasing or decreasing the size of the group.

4. When the volume per fish is the same for grouped and isolated fishes the difference in oxygen consumption is not of statistical significance.

5. Reasons for the "group effect" are not clear at present, but such factors as accumulation of carbon dioxide or reduction of oxygen tension do not appear to be important, since this effect appeared before these became limiting factors. Investigations are now in progress to determine the nature of this phenomenon.

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THE DEVELOPMENT AND SURVIVAL OF SPECIES AND VARIETIES IN PLANTED PASTURES

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In the more densely populated sections of the eastern and central states, planted pastures of grasses and legumes are gradually replacing the pastures which have developed without planting. As a result, research workers are studying the management of planted pastures. A problem receiving little attention is the testing of various seeding mixtures by means of field sampling methods. Two important questions arise in regard to the stand resulting from a given seeding mixture: percentage of germination and establishment of each constituent of the mixture, and effect of the presence of one species or variety upon the establishment and development of another. In order to obtain quantitative data on these questions, list-count, chart and clipped quadrats were used to study the percentage of survival, the general development, and the interaction of the species and varieties of twelve pasture mixtures.

The investigations of Hanson ('29) have a direct bearing on the question of survival. In studying the effect of different grazing treatments on eight pastures, he determined the number of viable seeds and calculated from the results of list-count quadrats the percentage of survival at the end of the first and second years. In one well-managed pasture he found that at the end of the second year, orchard-grass plants formed approximately 63 per cent of the total number of plants. As a result of the early dominance of orchard-grass, stands secured with 30 pounds of seed per acre were as good as stands secured with 50 pounds. Fenton ('27–'28), by the use of separation studies from small list quadrats, summarized the effect of improper and insufficient grazing on established Devon pastures. The percentage of each species present, including the weeds, gave some hint of the effect of the interaction of the plants. These investigations indicate the practicability of the more general use of various quadrat methods in the study of planted pastures.

Ecologists working in natural communities often find several species with different vegetative characteristics growing together without noticeable competition. Roberts ('28) states that " The rich pastures of the Midlands may well owe their stability not merely to isolation from the virgin plant association, but to a gradual natural selection of those forms of grasses and other plants which are most suited to the treatment in vogue, including grazing." This complementary relationship is also evident in planted pastures. Wiggins ('23), working in New York, found that in order to secure the best results, meadows should never be seeded to grasses alone, even if a pure stand of grass is desired. A better stand was always secured if clover was included in the mixture. Montgomery ('14) noticed that timothy grown in a mixture with clover was more luxuriant and was richer in nitrogenous compounds and concluded that there is little competition between the two species because the legume roots occupy a deeper stratum of soil. Fisher ('26), in discussing the pasture situation in Indiana, stated that mixtures are more satisfactory than pure seeding plots and that timothy and alsike clover make the cheapest mixture because of the rapidity of growth during the first few seasons.

At many stations extensive research is being conducted on problems which have an indirect bearing on the survival and development of the individual plants in planted pastures. This research includes work on the problem of fertilization, Archibald ('30), Archibald and Nelson ('29), Sprague ('29); on the rebuilding of worn-out pasture lands, Graber ('28), Sampson ('13), Stevenson *et al.* ('24); on the relation of organic food reserves to plant development, Graber ('28, '31), Graber *et al.* ('27), Stapledon ('27); and on the determination of species and varieties of grasses and legumes for planting mixtures, Montgomery ('14), Sampson ('13), Wiggins ('23).

MATERIALS AND METHODS

This problem was initiated in the fall of 1929 on plots which had been planted in the spring of 1928 by the Farm Crops Section of the Iowa Agricultural Experiment Station. Twenty-eight species and varieties of grasses and legumes were planted in pure seeding plots and in twelve different mixtures. One set of plots was planted at the college dairy farm where the plots were grazed. The other set of plots was planted in nearby experimental fields where the effect of the frequency of cutting was studied.

Each different mixture was denoted by a letter. This letter together with the contents of each mixture is shown in table I. The single-species plots are usually referred to by the species planted. Each mixture and each single-species plot was in triplicate. Mixture plots for grazing were 22 by 75 feet; the grazed single-species plots were 8 by 15 feet. The smaller plots for clipping were so arranged that half of each plot could be easily cut with a mower, leaving the other half for the check plot. These clipping plots were about 12 by 35 feet (mixtures), and 12 feet square (single-species).

With the exception of the data from the clipped quadrats all of the material presented in this paper was obtained from quadrats on the plots which were being grazed. In the fall of 1929 list-counts were obtained from six permanent meter quadrats in each mixture (two from each replication). These quadrats were laid out after a comparison had been made of the results from list-count quadrats located at random, with those placed in areas considered to be representative. As a result of this comparison it was decided to place the permanent meter quadrats in opposite corners (S–E. and N–W.) of the plots. A distance of two meters was left between the quadrat and the borders of the plot in order to overcome the border effect caused by the 12-inch space between the plots. All of the quadrats were marked off by means of wood strips and had an inside measurement of one square meter.

In making the list-counts the same worker counted each separate grass and legume plant in every four-square-decimeter area and these figures were recorded by an assistant. Greater accuracy in counting was made possible by the presence of the single-species plots, since the vegetative characteristics of these plants could be observed and compared with those in the mixtures.

As a basis for determining the percentage of survival of the several species the number of seeds per gram was determined from samples of the original seed. The percentage germination for each of the twenty-eight grasses and legumes had been previously determined.[1] From these data and the list-count data, the approximate number of the various kinds of seeds falling on a square meter area was calculated.

The first chart quadrats were obtained as soon as growth began in the spring of 1930. The chart quadrats were obtained from the permanent quadrats used for the list-counts. When the grasses and legumes were small the basal area was charted. After the plants had reached vegetative maturity the top cover was charted. The quadrats were charted on engineer's E4 graph paper, using various colors to represent the area covered by different plants. Later the number of squares that each species occupied on the graph was counted and the percentage of area covered was determined. Accurate charting of separate grasses was not always possible. Small, poorly established plants, closely associated with larger ones, were charted with them as one clump.

The separation studies were made by clipping one representative meter quadrat from each of the three replications. The quadrats were located, at random, in areas which appeared to be representative of the entire plot. The grasses were cut with a small hand sickle and the species were carefully separated. The separations were then dried in a steam drier for at least 24 hours. The grasses and legumes were weighed on a scale which was accurate to 0.05 of a pound. In addition to the one quadrat in each replication from which the species were separated, two additional quadrats were clipped from each replication and dry weight was determined. One quadrat was cut from each single-species plot.

COMPARISON OF THE MIXTURES

List-count quadrats. From September 20 until November 10 two one-meter quadrats had been counted from the three replications of the mixtures which were being grazed. In table I is presented a summarization of the list-counts obtained from six of the representative mixtures. No counts were made in mixture *L* because of the inability to distinguish between

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[1] These data are used through the courtesy of F. S. Wilkins, Assistant Chief in Forage Crops, Iowa Agricultural Experiment Station.

the juvenile forms of the sixteen different species planted. The data seem to indicate that for a given area there is an optimum number of similar plants that the area can support. This is shown by the constancy in the number of grass and legume plants in each mixture, regardless of the amount of seed planted.

TABLE I. *Analysis of seeding mixtures and the resulting survival after grazing, as shown by the list quadrat method*

	SEEDING			SURVIVAL AT END OF 2D SEASON			
	Rate of planting						
Mixture and species	Lbs. per acre	Viable seeds per square meter	Plants surviving	Per cent survival of viable seeds	Grasses	Legumes	Total
A. Timothy	8	2361	66	3.0			
Red clover	7	393	67	17.0	66	67	133
B. Timothy	4	1181	51	4.3			
Red clover	4	225	45	20.0			
Alsike clover	2	337	20	6.0			
Blue-grass	7	1966	65	3.3	116	65	181
C. Timothy	4	1181	57	4.8			
Red clover	4	225	34	15.0			
Alsike clover	2	337	18	5.3			
White Dutch clover	2	382	15	3.9			
Brome	7	217	12	5.5	69	67	136
G. Timothy	2	590	36	6.0			
Red clover	3	138	24	17.5			
Alsike clover	1.5	300	15	5.0			
White Dutch clover	5	286	14	4.9			
Alfalfa	3	125	25	20.0			
Blue-grass	3	843	29	3.4			
Brome	3	93	5	5.4	70	78	148
H. Timothy	2	590	37	6.3			
Red clover	3	138	23	17.6			
Alsike clover	1.5	300	16	5.2			
White Dutch clover	1.5	286	9	3.0			
Bi. Y. S. clover	3	140	0	0.0			
Blue-grass	3	843	37	4.4			
Reed Canary grass	3	910	11	1.2	85	48	135
K. Timothy	3	885	21	2.4			
Blue-grass	5	1405	14	1.0			
Orchard-grass	3	540	26	4.8			
Brome	3	93	5	5.4			
Meadow fescue	3	135	5	3.7	71	—	71

In all the mixtures except *K*, in which no legumes had been planted, the average number of plants per quadrat varied between 135 and 160. Within wide limits there seemed to be no correlation between the total amount, in pounds per acre, of seed planted and the number of plants surviving. The number of legume plants was approximately the same in every mixture, whether six or nine pounds of legume seed had been planted. The same constancy was evident among the grasses of the plots. This was strikingly illustrated by mixture *K*, in which 17 pounds of grass seed had been planted and yet the total number of grass plants surviving was no greater than in those mixtures in which only one-half this amount of grass seed had been used.

This inability of the grass seedlings to increase in number when large amounts of seed were planted is probably due to the fact that the upper soil layer had been completely occupied by the grass roots. When legumes are added their roots penetrate deeper, and consequently a mixture of grasses and legumes is more productive as a result of the greater plant population.

The *G* mixture showed an increase in the number of legumes present because of the high percentage of a second legume (alfalfa) added to the mixture. In this mixture the total number of blue-grass plants present decreased by about half, because of the establishment of the additional legume plants. In mixture *H*, in which biennial yellow sweet clover had been planted, the number of legumes was reduced the second year because of the inability of the sweet clover to reseed. The number of blue-grass plants in this mixture was slightly higher than in the former mixture, indicating that blue-grass was beginning to fill in the area previously occupied by the sweet clover. Wherever orchard-grass had been planted it formed large clumps, forcing the other species to form much weaker and smaller plants. Hanson ('29) found that orchard-grass formed such large clumps that other species were completely suppressed. He suggested that the amount of orchard-grass planted in any mixture should be considerably reduced.

The amount of seed planted in these mixtures was the same as that planted by the farmers of Iowa and is considerably less than that recommended by several stations. The percentage survival in the different mixtures shows that little thought is given to the total number of grass and legume seeds that may fall on a given area. In mixture *A* approximately equal amounts, by weight, of timothy and medium red clover seeds were planted. Although six times as many timothy as clover seeds fell on the same area, the total number of plants of each present at the end of the second season was almost identical. The difference between the viability of the seeds and the comparative vigor of the seedlings does not seem to warrant the planting of so many timothy seeds.

General Growth Relations. Beginning February 22, 1930, weekly records were made of the growth habit and response of the various grasses and legumes. In almost every instance the grasses and legumes were hardier and more vigorous in the mixture plots than where sown alone. The grasses seemed to grow better with the legumes and the legumes to be benefited by the permanent cover afforded by the grasses. After the January and early February snow had disappeared the wind removed a large part of the dead cover, and the results of winter-killing became evident. The alternate freezing and thawing, accompanied by the usual March winds, contributed to the winter-killing.

On April 19, the medium red clover was about one and one-half inches high, but the plants in the pure seeding plots had fewer and smaller leaves than those in the mixtures with timothy. On May 5, the white Dutch and wild white clovers were still too short for grazing. In every case where the legumes were planted separately they were beginning to be crowded out by weeds and small bunches of blue-grass. There were no weeds in the mixture plots, and in the plots where blue-grass had been included with taller grasses its clumps were small and usually contained only a dozen or more leaves.

Chart Quadrat Studies. From March 8, 1930 to October 20, successive chart quadrats were made from the permanent quadrats. When the first of these quadrats were made there was very little overlapping of any of the varieties and species in the mixtures containing two or three species. This is shown in mixtures *A* and *B* where there was very little overlapping of the different species. Figure 1 shows that as more species of grasses and legumes are added there is considerable overlapping of vegetative growth and the species are not so evenly distributed.

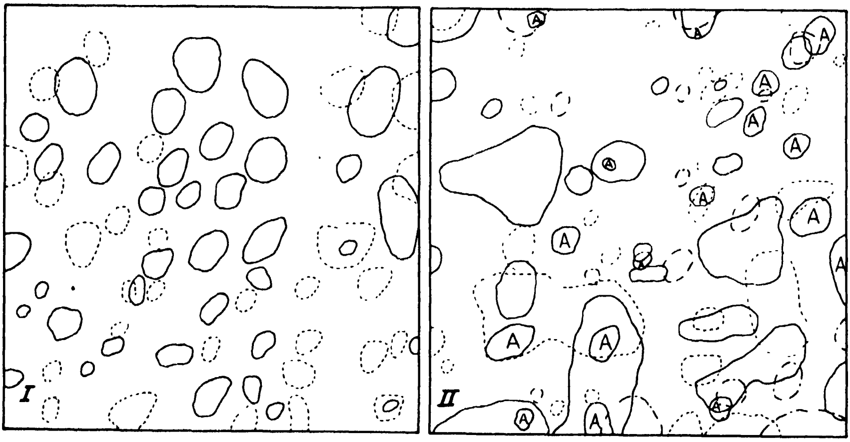

FIG. 1. Quadrat I contains a mixture of timothy and red clover and quadrat II a mixture of timothy, red clover, alfalfa and blue-grass. The quadrats, charted in March before much growth had taken place, show more overlapping where additional species had been planted. Timothy, solid line; clover, dotted line; blue-grass, dash-and-dot; alfalfa (A).

The second of the series of successive chart quadrats was made about May 27. These quadrats were charted in seven of the most representative mixtures, at about the time the grasses and legumes had reached their maximum height, and when most of the legumes were beginning to flower. The area charted was at the height of the greatest spread of the plants. This method of charting is much less indicative of plant relationships than the basal-area method, because it does not show accurately the exact area covered by any one particular grass or legume. It does, however, give a relative conception of the importance of the various species present, and is especially valuable in plots which from casual observation appear to be dominated by a single species. Tall meadow oat-grass in mixture *L* (fig. 2) appeared from a distance to be the dominant species, but chart quadrats showed that this plant constituted only five per cent of the total plant cover.

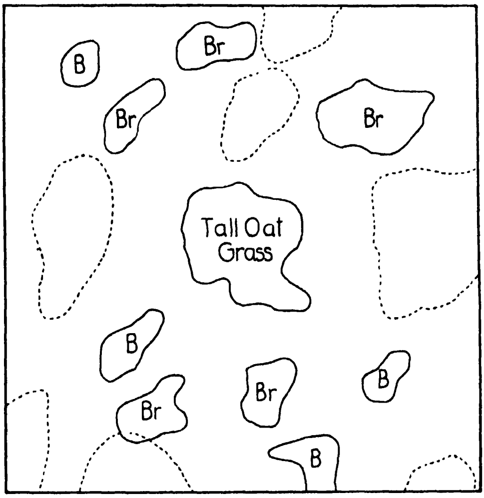

Fig. 2. A representative quadrat at maturity from mixture *L* containing 16 different varieties and species of grasses and legumes. From a distance tall meadow oat-grass appeared to be the dominant species. Clover, dotted line; brome grass, Br.; bare area, B. Orchard-grass is the dominant species comprising most of the cover in the uncharted areas.

Chart quadrats were made in these mixtures in October following the scanty fall rains. All the legumes were dead, and none had reseeded. Many of the grasses had been killed by one of the most severe and enduring droughts known in this section. Especially in those mixtures in which blue-grass had originally been planted, it was beginning to cover a greater part of the quadrat than was occupied by any other grass. In figure 3 charts made from the same quadrat in March and October are compared. The rapid spread of blue-grass and a complete dropping out of the clovers is evident.

The data obtained from the chart quadrats show that during the early spring the percentage of area covered by the plants is quite constant for all the mixtures, except *A*, in which timothy and medium red clover were the only species planted. This is in agreement with the list-count quadrat data obtained earlier. This seems to indicate that the total vegetative cover supported by any given area was limited by the physical conditions of the habitat, particularly by the water content of the soil and not by the number of kinds of grasses and legumes planted.

On March 8 average quadrats in mixture *A* contained 21 per cent timothy and 14 per cent red clover. In addition to timothy and red clover, blue-grass had been included in mixture *B*. In this latter mixture timothy was 18 per cent of the cover, red clover 9 per cent, while blue-grass occupied 13 per cent of the area of the quadrat. At this time blue-grass occupied about 15 per cent of the area in all plots where it had been planted. Where blue-grass was planted the area covered by timothy was reduced from 5 to 10 per cent, as compared with those plots containing timothy and no blue-grass. In the mixtures containing orchard-grass the total amount of bare area is somewhat reduced because of the large clumps of this grass. In this case the amount of clover present is considerably reduced. These comparisons seem to indicate that clover is much better adapted to growing with timothy and brome than with grasses producing large clumps.

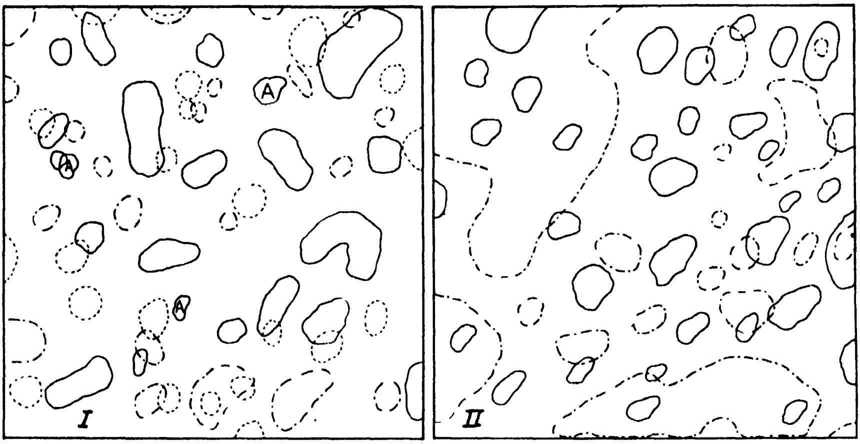

FIG. 3. An average quadrat from mixture *B* in which basal area was charted. Quadrat I was charted in March and quadrat II was charted in October following a very severe drought. Note the complete dropping out of the clovers and a very decided increase in blue-grass. The increased stand of blue-grass brings about more overlapping of vegetative forms. Timothy, solid line; clover, dotted line; blue-grass, dash-and-dot, alsike (A).

During the extremely dry season in which this study was made, the species and varieties of grasses seem to compete with one another on more nearly equal terms than do grasses and legumes, since in those quadrats containing both grasses and legumes, the grasses survived at the expense of the legumes. That the grasses seem to be able to survive under more severe competition is shown by the fact that there was less available soil moisture in the upper two feet of the soil in mixture *K* than in mixtures containing legumes. The soil moisture from the third and fourth foot was much less in mixtures containing legumes. In mixtures of grasses alone moisture at this depth was not used until later in the season under the conditions of this experiment.

The few quadrats which were charted from the clipped plots showed that the check plots at maturity contained much less blue-grass and more legumes and grasses than did the same plots which were being cut more frequently. As is generally known, blue-grass enters very rapidly whenever legumes and other grasses are subject to severe treatment.

The quadrats that were charted on October 25 showed more accurately the relationship that exists between the various grasses and frequency of cutting. Frequent clipping caused a decrease in the amount of timothy and orchard-grass present, with an added increase in the percentage of blue-grass. In mixture *A* the timothy occupied only 15 per cent of the total area in the section of the plot that had been cut frequently, in comparison to 30 per cent in the check section. This large bare area offers much space in which blue-grass and annual weeds can gain entrance and made rapid progress toward extermination of the timothy. In mixture *B*, 54 per cent of the area in the frequently clipped quadrats contained blue-grass, in comparison with 24 per cent in the quadrats from the check plots. Timothy occupied 8 per cent and 12 per cent, respectively. This comparison is shown in figure 4.

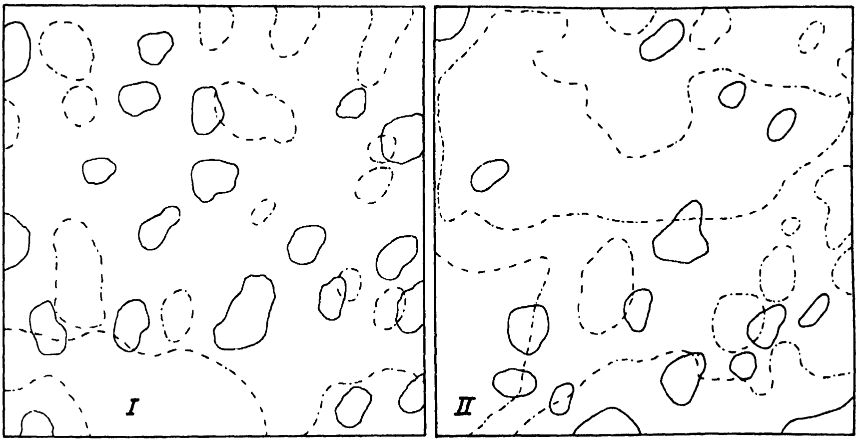

FIG. 4. The effect of frequent clipping on grasses and legumes in mixture *B*. The quadrats were charted following the drought and give basal area except for the blue-grass where bare areas within the stand were too small to chart. Quadrat I was made in the check plot and quadrat II in the frequently clipped plot. Blue-grass covers only 24 per cent of the area in quadrat I as compared with 54 per cent in quadrat II. Timothy, solid line; clover, dotted line; blue-grass, dash-and-dot.

Separation Studies. Separation studies were made in all the mixtures on which the effect of the frequency of cutting was being made. Because of the late, cool, dry spring none of the grasses and legumes made a great deal of early growth. The first separations were made on May 29 from those plots which had been cut frequently the previous season. During the preceding year (1929) the check plots had been cut twice and the frequently clipped plots had been cut five times. These plots and the checks were clipped about July 8. It had been the plan to clip the frequently cut plots at least four times during the season and the check plots twice, but because of the severe drought none of the plants from either treatment showed appreciable growth from July 10 until after October 1. The data given in table II are averages of percentage calculations from the three quadrats which were cut from each replication. In this study no attempt was made to separate any of the clovers because of inaccuracy of weighing such small samples, especially when dry. Some of the grasses were not accurately separated because they were not in the flowering stage.

TABLE II. *Separation studies (1930) from the check plots and those cut frequently showing a comparison of the yield of the various species on a dry weight basis in pounds. The clipped plots were cut May 29 and July 9, while the check plots were cut once on July 9*

Mixture	Treatment	Timothy	Clovers	Blue-grass	Orchard-grass	Alfalfa	Total
A	Clipped	.74	.41				1.15
	Check	1.38	.22				1.60
B	Clipped	.25	.29	.46			1.00
	Check	.74	.45	.29			1.48
C	Clipped	.88	.32				1.20
	Check	1.17	.23				1.40
G	Clipped	.35	.31	.46		.31	1.43
	Check	.75	—	.34		.68	1.77
H	Clipped	.43	.32	.46	—		1.21
	Check	.76	.20	.17	.52		1.65
K	Clipped	—	.10	.04	.79		.93
	Check	.32	.03	—	.73		1.08
L	Clipped	—	.23	.28	.71		1.22
	Check	.68	.22	.32	.26		1.32

Clover seems to be able to grow rapidly during the early part of the season, even when cut frequently, but the yield from later cuttings is unimportant. The weight of blue-grass obtained from the first separation studies on quadrats is in general a very good indication of how blue-grass enters when other plants are clipped frequently.

From the data in table II it is evident that frequent clippings reduced the yield. The total yield from the plots which were being clipped frequently was quite constant, regardless of whether the mixture contained an equal number of grass and legume plants, or a greater proportion of grass plants, except in mixture *K* composed entirely of grass plants. Under the more favorable conditions of the check plots, those plots with equal representation of grass and legume plants yielded slightly more than those in which the legumes were being crowded out by such grasses as orchard-grass and tall meadow oat-grass which form large clumps. Mixture *K*, in which no legumes were planted, seems to fall in a separate category. In this mixture both the chart-quadrat data discussed previously and yield data give no conclusive results which could be interpreted as due to frequent clipping.

The data given in table III are averages from the clipped quadrats in the single-species plots. Weeds were very abundant in the legumes. None of the single-species, except alfalfa and Reed canary grass, yielded as much as mixtures from the check plots. Medium red clover, alfalfa, timothy, redtop, Reed canary grass, orchard-grass and tall meadow oat-grass yielded much more than any of the other species, but these failed to yield as much as any mixture of grasses and legumes in the check plots. Table III shows that many of the grasses and most of the legume plots were so short or so badly infested with weeds that no quadrats were clipped on July 8.

TABLE III. *Total dry weight of clipped quadrats obtained from pure seeding plots of grasses and legumes*

	Cut frequently			
Variety	May 29	July 8	Total	Total Check
Medium red	.84	.38	1.22	1.10
Alsike	.46	(weeds)	.46	.48
White Dutch	.13	"	.13	(weeds)
Ladino	.24	.22	.46	.44
Wild white	.06	.16	.22	.18
Wild red	(all dead)			
Alfalfa (Grimm)	.58	.60	1.18	1.56
Bi. Y. Clover	(all dead)			
Timothy	.44	.22	.66	.98
Ky. Blue-grass	.36	(weeds)	.36	.47
Bromus inermis	.60	.20	.80	.76
Canada blue-grass	.43	(short)	.43	.90
Reed canary	.70	.42	1.12	1.41
Orchard-grass	.42	.29	.81	.95
Redtop	.52	.31	.83	1.06
Other fescues	.42	(short)	.42	.86
Perennial rye-grass	(none available)			
Tall oat-grass	.60	.30	.90	.97
Crested wheat-grass	.68	(short)	.68	.72
Western rye-grass	.32	.27	.59	.78
Meadow fescue	.48	.31	.79	1.06

The writers are especially indebted to Professor F. S. Wilkins of the Farm Crops Section and to Dr. C. Y. Cannon of the Dairy Section for permission to make this study on their plots and for some assistance received from the Farm Crops Section in collecting the data for the separation studies.

SUMMARY

List-count, chart and clipped quadrats were used to study the reaction of different species and varieties of grasses and legumes in pure seeded plots and in mixtures.

Under the conditions of this investigation list-count quadrats revealed a remarkable constancy in the total number of grass and legume plants in all mixtures. Very slight variation in number of plants per quadrat resulted from the planting of different numbers of seed; within limits of 2300 and 7700 seeds per meter quadrat. This seems to indicate that for a given area there is an optimum number of plants of similar requirements that the area can support.

In the early spring, legumes planted with grasses appear to be hardier than the same legumes planted separately. This is undoubtedly due to the protection afforded by the more persistent dead stems and leaves of the grasses.

Mixtures containing two or three different kinds of pasture plants showed much less overlapping of individual plants than did those containing more than three different types of plants. This was shown by chart quadrats obtained when the plants were relatively small.

Chart quadrats taken at maturity were generally not so clearly indicative of the relative importance of the species as those charted during early vegetative growth. However, these quadrats show the relative importance of tall, infrequent species.

Severe drought seems to weaken most of the grasses and to kill out the clovers because of their inability to reseed under such conditions. Blue-grass enters in increased quantities during wet periods following a severe drought.

Separation studies showed that similar mixtures of grasses and legumes produced about the same dry weight per quadrat. Mixtures of grasses did not yield so much as did the mixtures containing grasses and legumes. No quadrats from the single-species plots yielded as much as any of the mixtures.

From the results of clipped quadrats the effect of frequent clipping was less evident in single-species plots and in mixture *K*, containing no legumes, than in mixtures of grasses and legumes. Competition appeared to be so keen between the individual plants of a single species when planted alone that frequent clipping did not seem to materially decrease the yield as compared with the check plots. This was more evident in plots of single-species of grasses and in mixtures of grasses than in plots of single-species of legumes. This is probably the most striking indication of the complementary relationship existing between grasses and legumes in a mixture.

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THE ROOT SYSTEM OF LONGLEAF PINE ON THE DEEP SANDS OF WESTERN FLORIDA

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The most extensive timber type on the Choctawhatchee National Forest, 30 miles east of Pensacola, Florida, is longleaf pine, *Pinus palustris.* The stands consist of a sparse growth of 8 to 10 mature and overmature longleaf pines to the acre with an understory of turkey oak, *Quercus catesbaei,* and bluejack oak, *Q. cinerea.* Understocking of pine, while resulting in part from past logging practice and frequent fires, may also be attributed to natural causes, among which insect attacks, drought, and poor site have played no small rôle. In addition to causing the gradual depletion of the veteran trees, these adverse conditions have made natural replacement inadequate, so that the present forest is on the decline (fig. 1).

As the Choctawhatchee region is typical of approximately five million acres in the state of Florida, and as timber growing appears to be one of the most logical means of utilizing this large acreage of sandy land, the importance of a study of reforesting these lands with desirable tree growth has been recognized.

The most widespread soil of the region is classed as Norfolk sand, deep phase. This sterile sand, in places 60 feet deep, is 96 to 98 per cent silica. Because of the small amount of fine material present, the normal moisture holding capacity is approximately only 5 per cent. Drainage is excessive over most of the area. The average annual rainfall is 65 inches, and is fairly evenly distributed throughout the year with the exception of late spring or early summer when dry periods of 3 to 6 weeks duration may occur. That fires have been common in this region is attested by the numerous turkey oak sprouts. A sparse ground cover exists, consisting of wire grass, *Aristida* sp., other herbaceous plants including a variety of legumes, and the gopher apple, *Chrysobalanus oblongifolius.* Pine reproduction is rarely present in sufficient density to insure normal stocking. On abandoned fields, however, reproduction is much more abundant, indicating that climatic and edaphic factors are probably not the only ones unfavorable to the regeneration of longleaf pine.

One phase of the work on the natural reproduction of longleaf pine in this region is a study of the roots of trees varying in size from seedlings to mature trees, the older trees being included as a means of judging whether root competition from these individuals is a factor in seedling survival. Although this work has not been completed, the observations already made are believed to be of sufficient general interest to be reported at this time.

AREAS STUDIED

Trees were excavated on three sites: (1) an old field abandoned 12 years ago; (2) an area supporting a stand of longleaf pine and turkey oak judged to be typical of the Choctawhatchee region; and (3) a poorly drained area adjacent to a swamp. The old field was selected because of the absence of any vegetation other than longleaf seedlings, scattered turkey oaks, live oaks, *Q. virginiana,* and a sparse ground cover of grasses. It was believed that

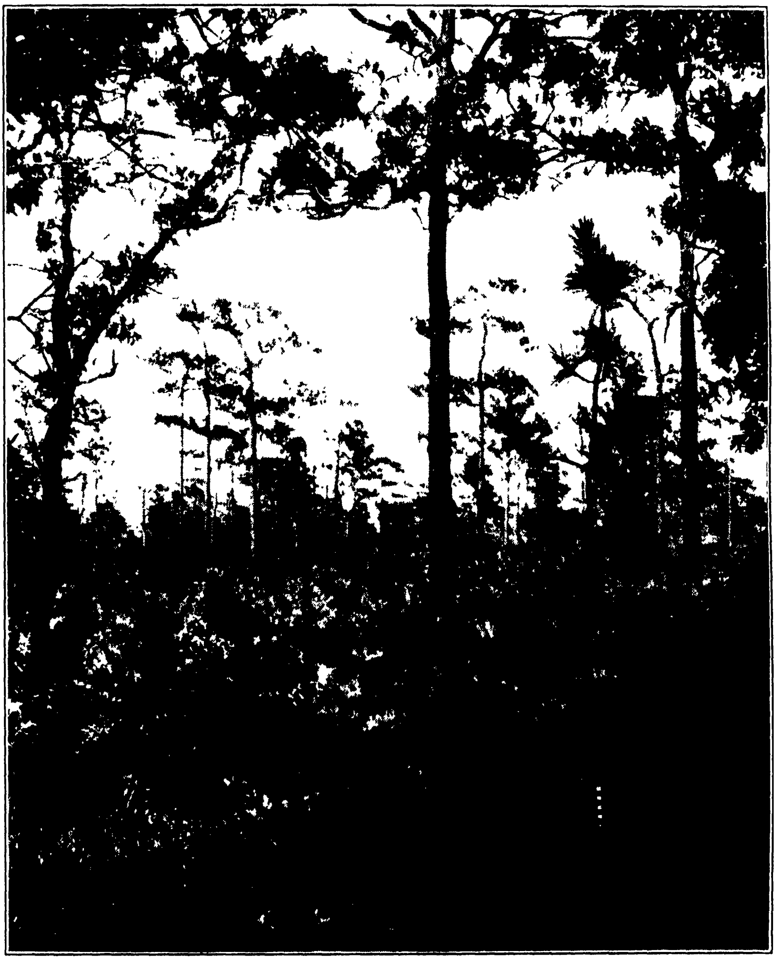

FIG. 1. A typical stand of longleaf pine and the commonly associated turkey oak on deep sandy soils in Florida. (U. S. Forest Service Photograph.)

root competition would be at a minimum, and hence the pine seedlings would presumably show the normal root development of the species for this particular site. The soil and drainage conditions of the longleaf pine-turkey oak area and the old field appeared to be very similar. Because of the loose structureless nature of the sands in this region, it is difficult to detect any difference between virgin soils and soils of abandoned cultivated fields except for a slight difference in color at the depth of plowing in the field soils. On the third area, characterized by poor drainage, the soil was medium sand 12 to 14 inches deep, underlain by a slightly mottled orange-yellow sandy clay. At the time of the present study, the water table was about 28 inches below the surface. The forest cover was longleaf pine.

FIELD WORK

Six seedlings (trees less than 3 feet in height) were excavated from the old field. Following this, seven seedlings, one sapling 11 feet tall, and one mature tree were examined in a nearby longleaf pine-turkey oak stand. Three seedlings from the poorly-drained site were examined. A trench about 2½ feet wide and from 8 to 10 feet long was dug at a distance of 3 feet from each seedling selected for examination. The working wall was caved in by carefully digging with a set of dull pointed sticks. When the taproot had been completely exposed, it was photographed and sketched. The lateral roots were then uncovered by the same process and measurements and sketches were made of each. In this manner, practically all the roots from each tree were followed to their extremities. Those destroyed were a few vertical roots which were cut in digging the ditch. The horizontal roots which were severed were traced to their ends and sketched. No attempt was made to trace the vertical roots which branched from these.

After being completely excavated each seedling was taken to the office, where it served as a check in the preparation of final pen-and-ink sketches, based on field sketches, showing the seedling both in vertical and in horizontal section. Lastly a map was made showing all woody plants over 6 inches in height within a distance of 12 feet of each seedling.

Before the excavation of the mature tree was begun, the lateral roots were cut off at a distance of 5 feet from the stem, and the tree was felled. A hole 20 feet in diameter at the top and 15 feet in depth was dug in an attempt to expose the taproot so that photographs and measurements could be taken. As the sandy soil caved in just when the tip of the taproot was reached, the entire stump was removed by means of a tractor. Because of the great labor and time involved, only one lateral root was traced.

ROOT SYSTEMS OF SEEDLINGS ON WELL DRAINED SANDY SOIL

The typical root system of a young longleaf pine between 3 and 30 inches in height was found to consist of three distinct elements: (1) a prominent taproot; (2) a set of horizontal roots consisting of 9 to 11 laterals[1] and a varying number of sublaterals; and (3) a series of vertical roots which branched from the laterals. Each of these types was found on every tree examined.

The Taproot. The taproots varied from 34 to more than 108 inches in length, with an average of about 60 inches (table I). The fact that the taproot of tree X was only 34 inches long was the result of its having been severed by a pocket gopher, *Geomys* sp. A wound callus had formed at the extremity, and from this three adventitous roots were growing. These were 12 to 18 inches long, and serve as an interesting example of the recovery of the taproot following an injury. Tree VII, with a 36-inch taproot, showed abnormal branching near its extremity. Tree XI, with a taproot of only 40 inches, also branched to an unusual degree. Tree XI was further characterized by unusually long lateral roots, a condition which may possibly have been reflected in the poor development of the taproot. Neither of these trees was considered to be typical.

TABLE I. *Longleaf seedlings excavated Choctawhatchee National Forest*

Area	Tree Number	Height	Length of taproot	Length of 3 longest laterals	Total laterals	Laterals within first foot of soil	Maximum depth at which a lateral branched from taproot
	Number	Inches	Inches	Inches	Number	Number	Inches
Old field	II	3	67	60, 39, 34	10	8	15
	III	5	51	60, 50, 32	12	9	22
	V	9	62	86, 76, 72	11	10	29
	IV	11	58	87, 64, 55	13	12	27
	I	13	108+	138, 120, 102	10	7	12
	VI	27	63	100, 90, 84	12	11	17
Longleaf-turkey-oak type[1]	X	8	34	70, 70, 58	9	9	5
	XII	10	71	134, 74, 70	16	13	25
	VII	11	36	102, 84+, 84+	11	9	14
	VIII	14	74	82, 80+, 70+	12	12	12
	XIII	14	75	98, 90, 70+	11	9	25
	IX	24	65	172, 120, 94	11	11	6
	XI	30	40	146, 112, 92	11	10	14
Poorly drained site	XVI	10	23	120+, 84+, 44	7	7	8
	XVII	16	22	146+, 135+, 75	13	13	8
	XV	30	29	130, 90, 40	10	10	9

[1] Tree XIV was a sapling 11 feet tall, which was only partly excavated.

At the other extreme in the development of the taproot was tree I which,

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[1] Throughout this paper the term *lateral* has been arbitrarily used to designate all horizontal roots exceeding 2 feet in length originating from the taproot. The smaller horizontal roots have been called sublaterals. Laterals were found to be concentrated entirely within the upper two feet of the soil, whereas the *sublaterals* branched from all portions of the taproot but largely at depths greater than two feet.

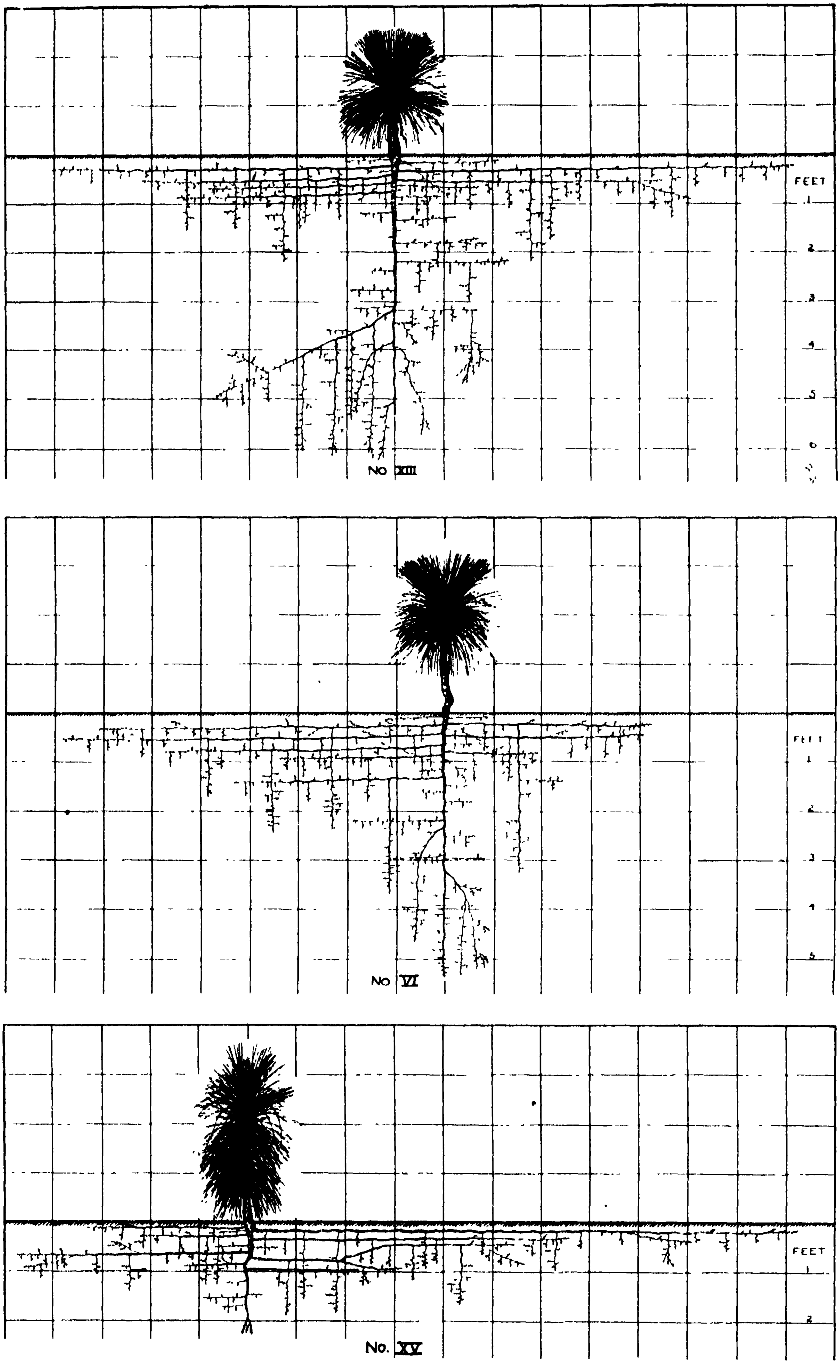

FIG. 2. Transect views of roots of longleaf pine seedlings. No. XIII from old field; VI from longleaf pine-turkey oak type; and XV from poorly drained longleaf site.

while only 13 inches in height, possessed a taproot over 9 feet in length. The root was broken off at this length and could not be traced further. It was obvious that the tip had been almost reached.

Trees VI and XIII (fig. 2) illustrate what is considered to be a normal development of the taproot. Their taproots were 63 and 75 inches long, respectively, and showed types of branching which were commonly found on the seedlings examined. The straight downward course of the taproot, with but minor deviations in direction, is typical for the trees examined.

Laterals and sublaterals. Perhaps the most striking characteristic of both the laterals and the sublaterals was their tendency to extend in a horizontal plane at a uniform depth throughout their entire length. Rarely were the tips of such roots at a greater depth in the soil than their points of origin at the taproot. The roots of almost all trees examined were distributed through the soil as if they were following a system of rectangular coordinates.

As seen from the plan views of the root systems (figs. 3–5), although the lateral and sublateral roots continued their courses in a horizontal plane, they frequently changed the direction of their growth within this plane. Roots growing in semicircles were not uncommon, although the general tendency appeared to be to grow in a straight line. One pine root which, after growing its first 4 feet in length, was obstructed by a 10-inch turkey oak, progressed around the oak to a point directly opposite and then continued on its original course in a projected straight line.

An interesting point regarding the lateral roots was their concentration near the surface of the soil (table I). Of the 179 lateral roots excavated, 160, or 89 per cent, occurred in the first foot of soil. This characteristic is illustrated by the seedlings shown in figure 2.

The length of the laterals varied from 2 feet (the arbitrary limit distinguishing laterals from sublaterals) to 14 feet, 4 inches. For tree VI and likewise for tree XIII the maximum lateral spread was approximately 15 feet (figs. 3, 4).

The number of laterals was surprisingly constant, as is seen from column 6, table I. Only two trees, numbers XII and XVI, had less than 9 laterals or more than 13.

The sublateral roots ranged in length from their arbitrary maximum of 2 feet down to a fraction of an inch. They were found to occur from a level just beneath the soil surface to the tip of the taproot. In contrast with the laterals, the sublaterals were more abundant below the 1-foot soil depth.

Vertical Roots. All the seedlings were characterized by a system of vertical roots distinct from the taproot. Several showed an unusual development of these roots which branched from laterals at distances as great as 6 feet from the stem and penetrated to a depth equal to that attained by the taproot. Several of the vertical roots developed a set of sublaterals equal in volume and number to those originating from the taproot. The

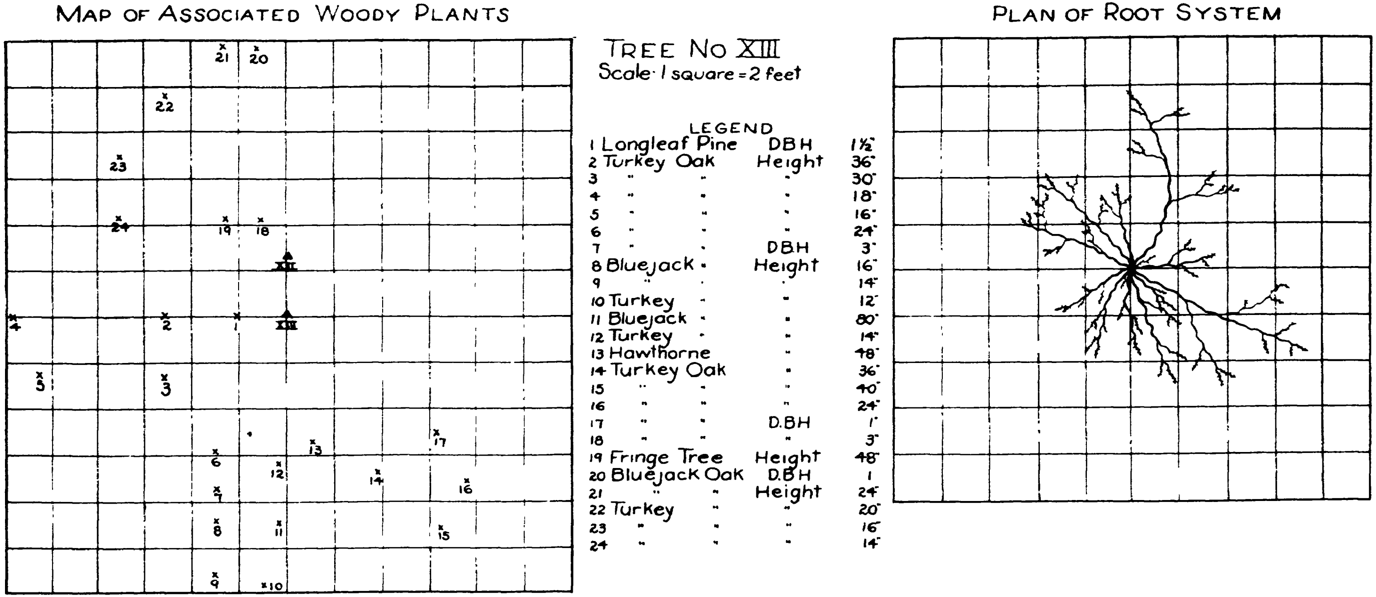

FIG. 3. Plan of root distribution of seedling No. XIII and map of associated vegetation.

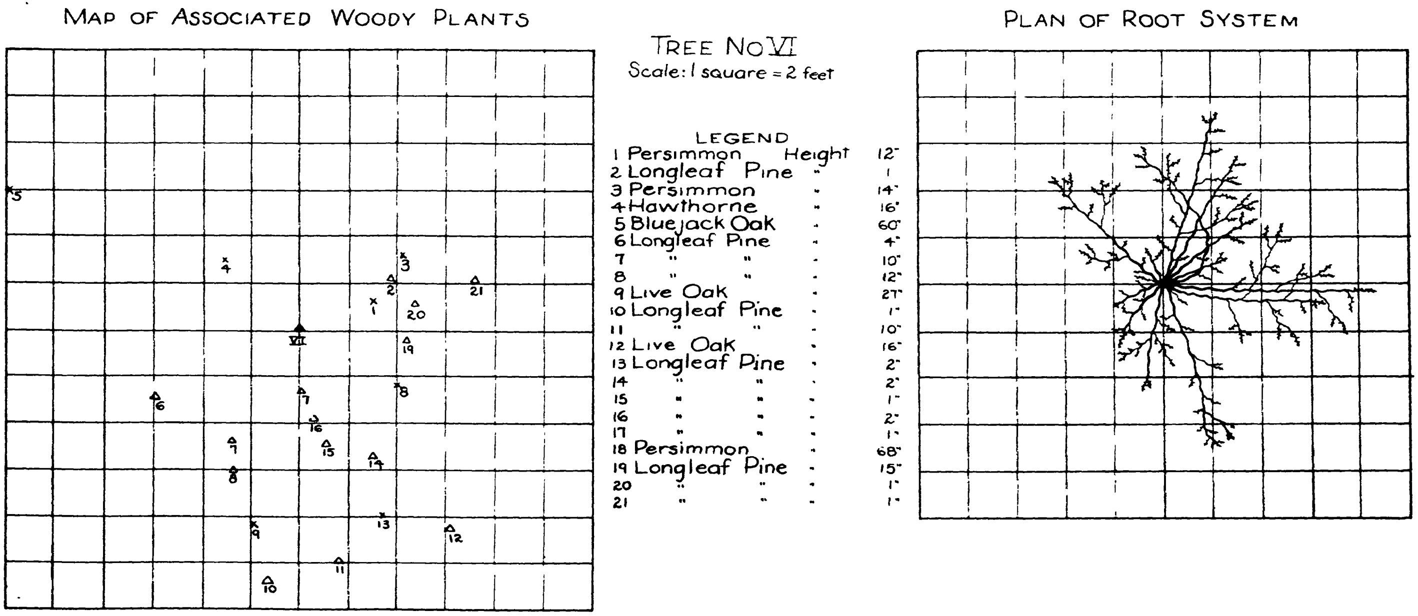

FIG. 4. Plan of root distribution of seedling No. VI and map of associated vegetation.

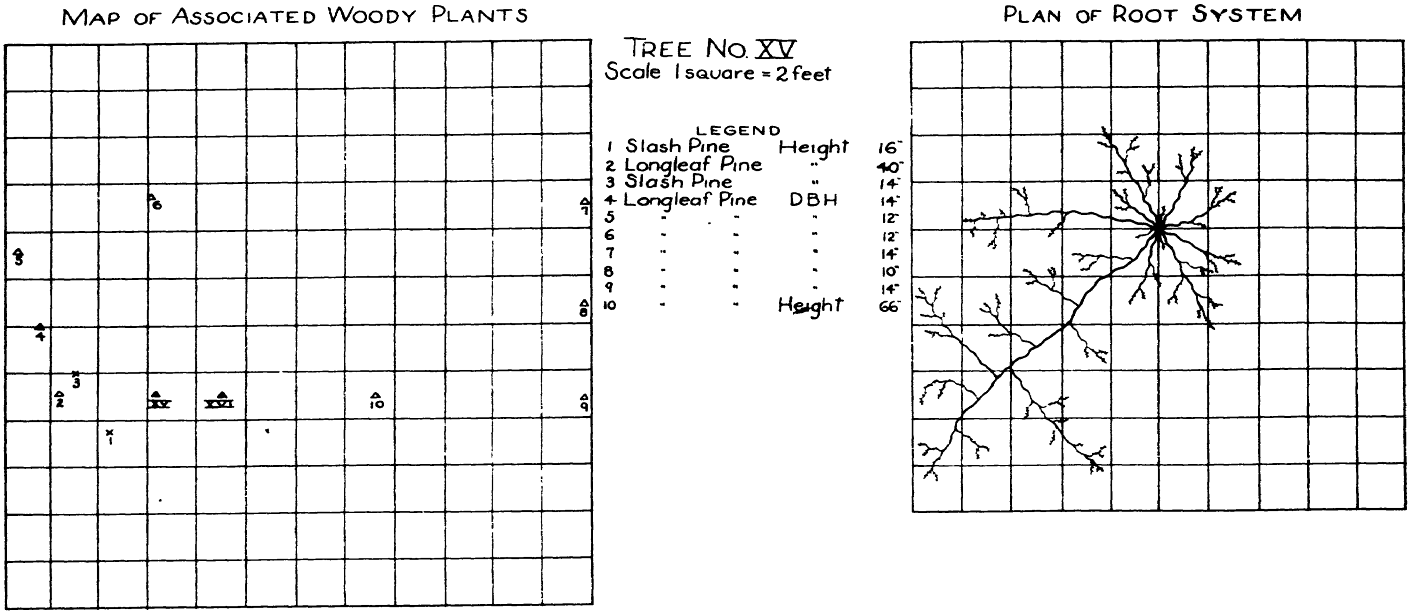

FIG. 5. Plan of root distribution of seedling No. XV and plan of associated vegetation.

vertical roots, like the taproots, penetrated downward in straight uninterrupted courses.

Comparison of Root Systems of Seedlings from the Three Sites

The differences in root development of the seedlings from the three sites studied are clearly brought out by figure 2. The most striking contrast was in the taproots which on the poorly drained area were only 22 to 29 inches long compared to approximately 3 to 6 feet on the well drained sites. During the month of July, 1931, when this study was conducted, the water table of the poorly drained area was only about 28 inches beneath the surface. Obviously a high water table exerts an inhibitory influence upon the development of the taproot of longleaf pine.

The seedlings from the old field were characterized by shorter laterals than those from the other two areas. Such a difference is not surprising when these are compared to the trees from the pine-oak site where root competition was obviously more intense; but the long laterals found on the poorly drained area were not expected. Each of the three seedlings excavated from this site had at least two roots 7 feet or more in length. Competition for moisture was hardly a factor in the development of the seedlings on this area. Two lateral roots, on trees XV and XVII, after horizontal elongations of 2 and 5 feet respectively, ascended somewhat abruptly to a plane several inches nearer the surface, where they continued throughout their remaining growth.

Root System of Mature Trees on Deep Sandy Soil

Only one mature tree was studied and, because of the great amount of labor required, this was only partly excavated. This tree was approximately 250 years old. It was 54 feet high and 17 inches in diameter 4½ feet above ground.

The Taproot. The massive taproot, typical of longleaf pine growing on well drained sites, is shown in figure 6. At a depth of 13 feet 4 inches, this root divided into two stout branch roots each 3 inches in diameter, the longer of which ended at a depth of 14 feet 2 inches. Several cordlike roots from ¼ to ½ inch in diameter continued downward from each of these branch roots, but, as they were broken when the stump was removed, their lengths were not determined.

Supplementary taproots. The term "supplementary taproot" has been applied to rigid, sturdy vertical roots from 4 to 5½ feet in length and from 3 to 5 inches in diameter at their upper extremity, because of the close similarity between their morphological characteristics and those of the true taproot. These roots originate from lateral roots as far as 5 feet from the taproot. Like the taproot, they may or may not divide at their lower extremities; in either event their ends are rounded and from ¼ to ½ inch in diameter. The number of horizontal roots originating from the supplementary taproots is much smaller than that from the taproots. It does not seem probable that these roots have an important part in the conduction of water or nutriments, because of the limited number of branch roots. That they are a factor in anchoring the stem there can be little doubt. Four such roots were found on the mature tree, two of them occurring on the same lateral and only 2 feet apart. All these possessed two or three horizontal branch roots.

To follow the trend in development of this type of root would have necessitated excavating trees intermediate in size between seedlings and mature trees, and this was not possible at the time. It seems likely that the conspicuous vertical roots found within 2 feet of the taproot of trees like VI (fig. 2) would have developed into supplementary taproots.

FIG. 6. Main and supplementary taproots of mature longleaf pine growing on deep sandy soil. (U. S. Forest Service Photograph.)

Because of the marked taper of the lateral roots within the first 10 to 15 feet, it seems improbable that supplementary taproots[2] could develop at a greater distance than 8 feet from the taproot.

No information was obtained regarding the vertical roots which branched from the laterals at greater distances from the taproot. From observations made elsewhere it is believed that these roots are similar in appearance to the horizontal roots and entirely lack the rigidity and stoutness of the supplementary taproots.

Laterals. An idea of the great extent of the lateral roots of mature longleaf pine was obtained by following one such root to its termination. The root selected was 6 inches in diameter, measured 2 feet from the taproot,

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[2] Supplementary taproots have been observed on trees elsewhere in the longleaf region on soils of various textures. This type of root is believed to be a characteristic development of longleaf pine.

and was the fourth largest in diameter of the 10 laterals present. This root grew at an average depth of approximately 10 inches beneath the surface of the soil to a distance of 71½ feet, at which point it changed direction abruptly and descended vertically to a depth of 3½ feet below the surface, where it ended. The end of this root was 51 feet, in a straight line, from the taproot. Fourteen feet from the taproot the root branched. The branch root had a length of 26½ feet. At 35 feet another branch occurred. It was this root which ended 71½ feet from the taproot. The main root was followed to a distance of 46 feet, when it ended abruptly while still 1 inch in diameter. The root had been severed in several places near its termination, presumably by pocket gophers.

The marked taper of the lateral roots within the first 10 or 12 feet has already been mentioned. At a distance of 12 to 15 feet from the taproot, the diameter of the laterals was approximately 1 inch. Beyond this, taper was very slight, being almost imperceptible in a section less than 10 feet in length. At a distance of 2 feet from the taproot the lateral roots ranged from 4 to 7 inches in diameter.

During the course of the excavation, 7 of the 10 laterals of this large tree were examined for a distance of 12 feet from the taproot. All occurred within 10 inches of the surface of the soil.

One type of horizontal root was found to originate both from supplementary taproots and from laterals. These roots appeared to have begun their elongation normally. At a distance of 2 to 6 feet from their point of origin, however, they changed their course abruptly so that their further elongation was toward instead of away from the taproot. Upon coming into contact with this root, they extended downward to levels 6 to 8 feet from the soil surface, always remaining in intimate contact with the taproot. The numerous small branches of these roots forced their way into the fissures and even into the scales of the outer layers of bark of the taproot. Below 4 feet the bark of the taproot became very thin and here these roots were found to be cemented to the taproot by some material which they secreted. So tenaciously did these fine roots adhere to the taproot that many were broken off when the larger root from which they originated was removed for examination. A possible explanation for the presence of these roots is that moisture conditions are more favorable in the soil immediately surrounding the taproot as it is likely that penetration by rain water or heavy dews is much greater there because of the water which follows down the exterior of the root.

SUMMARY

1. On each of three different sites from which roots were excavated, the root system of a typical seedling was found to consist of three well-defined elements: (1) a prominent taproot, (2) an extensive system of horizontal roots, and (3) a set of vertical roots distinct from the taproot.

2. Seedlings between 3 and 30 inches in height on well-drained soils were characterized by taproots 3 to 9 feet in length. The length of the taproots of seedlings on poorly drained soils was limited by the height of the water table.

3. The lateral roots of seedlings from the longleaf pine-turkey oak type were longer than those of seedlings from the old field. This was attributed to conditions of more intense root competition in the former type, caused by the presence of the turkey oak.

4. The total number of lateral roots on 15 of the 17 trees examined ranged from 9 to 13.

5. Approximately 90 per cent of all the lateral roots excavated occurred within a foot beneath the surface of the soil.

6. The taproot of a mature longleaf pine on a deep sandy soil was 14 feet 2 inches long. The diameter of this root 5½ feet beneath the surface of the soil was 17 inches, or the same as the diameter of the trunk 4½ feet above the surface.

7. One lateral root of the mature tree was 75 feet in length and was 6 inches in diameter at a distance of 2 feet from the taproot. Throughout its horizontal elongation the root remained approximately 10 inches below the surface. At a straight-line distance of 51 feet from the taproot this root turned abruptly downward. It ended at a depth of 3½ feet beneath the surface.

AN AMPHIBIOUS HABITAT ON VERTICAL SANDSTONE CLIFFS[1]

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The fresh-water pulmonate snails have been very generally considered as a group of originally aquatic molluscs which secondarily became adapted as land dwellers to air breathing and as a third step in their history returned to the water, still retaining the lung, reminiscent of their terrestrial past. Even in this relatively complicated series of habitat reversals the adaptation of the pulmonate snails is not complete nor final for many species are displaying a fourth stage in their readjustment to amphibious conditions of life. Several species of the Lymnaeidae are recognized as amphibious for they are encountered characteristically on the mud flats, that transition zone between the aquatic and the strictly terrestrial conditions. Thus, Baker ('11, p. 20) characterizes several species as semi-aquatic inhabitants of the mud flat zone. This horizontal junction of aquatic and terrestrial habitats is commonly the only one that is recognized as providing an amphibious environment. One of the few instances in the literature referring to perpendicular surfaces as providing the site for development of an amphibious environment is that described by Dr. H. A. Pilsbry ('26). This author (p. 325) described a new species of *Physa* from Zion National Park which had become established on and apparently is restricted to isolated areas on the vertical cliffs of the canyon walls where water seeps from joints along bedding planes. The present writer has discovered an additional instance of vertical cliffs providing the site for the development of amphibious snail colonies. This newly discovered locality is within the Turkey Run State Park, near Marshall, Indiana.

One of the most characteristic features of the Turkey Run State Park is the series of deep ravines (locally termed canyons) cut through Mansfield sandstone by the post-glacial action of the tributaries of Sugar Creek. Many of the tributary streams are now reduced to mere rills, except in periods of heavy rainfall, and during mid-summer some of them become converted into series of isolated pools intercommunicating by seepage of the water through the sand and gravel in the stream bed. For a number of years, the writer has studied the animal life of these streams. Though Sugar Creek carries a fairly representative molluscan fauna and the surrounding woodlands bear an abundant land snail population, molluscs are almost wholly lacking in the small streams and pools within the ravines.

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[1] Contributions from the Zoological Laboratory of the University of Illinois, No. 434.

In 1930, the writer observed a number of Lymnaeid snails clinging to the vertical sandstone cliffs, in areas moistened by the seepage of diminutive springs. Observations made at that time and subsequently failed to reveal any of the same snails either in the waters of the streams or along the banks. Series of collections have been submitted to Frank C. Baker who has identified the snails as *Fossaria modicella* (Say). At the time the first collections were taken, most of the snails were found in a flocculent iron deposit laid down around the seepage areas. Detailed field observations were carried on during the last week in August, 1932. In some of these later collections snails were found in abundance on relatively clean sandstone, bearing no surface accumulations and but barely moistened by the slight flow of water. In one collection, *Pomatiopsis lapidaria* (Say) was found associated with *Fossaria modicella* on the sandstone bluffs, the two species intermingled on the same seepage area. This offers additional evidence of the amphibious nature of *Pomatiopsis* to that recently summarized by Baker ('31, p. 489).

The face of the sandstone cliffs bearing snails was essentially vertical, though in many instances there was either a slight slope or an undercut. The areas where snails occurred bore no fixed relations to the streams. In some instances the stream washed the foot of the cliff where snails dwelt while in others the stream passed on the opposite edge of the wide flood plain, more than two hundred feet from the escarpment bearing the snails. Field observations were extended into every one of the deeper ravines of the park area and specimens were collected from the sandstone walls of every ravine. Relative abundance of the snails seemed wholly dependent upon relative development of the seepage areas on the vertical walls. Some colonies were large while others comprised but a few individuals. The regions between colonies were wholly barren of snail life and in some instances these barren stretches extended several hundred yards. In vertical distribution, the snails were found from stream level to a height of more than seven feet. Colonies of *Fossaria* were found at the head of one of the ravines at an elevation of more than one hundred feet above the level of Sugar Creek, and at least one hundred yards from the creek. This ravine carries no stream except following a period of heavy rains.

Surfaces in bright sunlight for part of the day seemed as well populated as undercut cliffs reached only by diffused light. A thin sheet of water flowed over the area occupied by some colonies while barely enough water to dampen the sandstone created the conditions under which other colonies lived. In addition to the flocculent iron deposits mentioned earlier, some of the habitats were characterized by the presence of a superficial limy residue left by the evaporation of the surface water. Several dead *Fossaria* shells were found bound to the sandstone by this limy material.

Nothing is known of the methods of dispersal of *Fossaria modicella* on the sandstone cliffs. The species is commonly recognized as amphibious so it is possible that at times of heavy rain and high water the boundaries of colonies are not so clearly marked as they are during mid-summer periods of drought. A search extending over a period of two years has failed to disclose the presence of any specimens of *F. modicella* in the streams of the area under investigation or on the stream margins under conditions described by Baker ('11, p. 19) as characteristic for the species. It seems that *Fossaria modicella* is here becoming adapted to a new type of amphibious habitat provided by the vertical walls with their seepage areas and has abandoned its customary dwelling place along the horizontal margins of streams and pools.

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THE DENSITY OF SPRUCE AND FIR REPRODUCTION RELATED TO THE DIRECTION OF EXPOSURE[1]

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In northern Europe difficulty of securing natural reproduction of Scotch pine, *Pinus silvestris* L., and Norway spruce, *Picea excelsa* Link., has led to the adoption of various forms of reproduction cuttings providing partial shade or protection to the seedlings from hot sun and wind. Echeloned strips or border-cuttings, with northeast exposure, originated by Wagner ('23*a–b*) in Germany, and applied successfully by Alarik ('25) and others in Sweden, have as their chief object, the protection of seedlings from too strong heat. On south and west exposures direct insolation and heat reflected from tree trunks often result in temperatures lethal to young seedlings (Hartley, '18; Bates, '24) and in desiccation of the surface soil so that even germination does not occur. On east exposures the sun is less injurious than on west due to the lower temperature in the early morning, related to higher humidity and presence of dew. Thus moisture is conserved on the north and east sides of a stand, and seedlings are protected from severe heat. Furthermore prevailing westerly winds in dry weather (when cones are open), blow seed toward the reproduction strips. For these reasons various arrangements of cuttings have been made in order to take maximum advantage of north and east exposures.

In northeastern United States summer temperatures are frequently higher than in lands where border cuttings have been found useful, and it seems probable that similar measures would be equally beneficial here. The presence of a dense, nearly pure, stand of red spruce, *Picea rubra* Link., in Dummer, New Hampshire, left isolated by clearcutting on all sides, furnished an opportunity for observing the reproduction on different exposures in order to determine whether the effect of exposure was important.

DESCRIPTION OF THE STAND

The stand was exceptionally dense old field spruce, composed of red spruce with a few scattering white spruce, *Picea glauca* (Moench.) Voss., and about 5 per cent balsam fir, *Abies balsamea* (L.) Mill., having a total volume of 7,120 cubic feet per acre. The average age at the time of observation (November, 1926) was 76 years, the average height of dominant trees 64 feet; and

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[1] Presented before the New Hampshire Academy of Science at Wolfboro, New Hampshire, May 28, 1932.

there were an average of 680 living trees per acre (and many dead ones) on an area of about 15 acres. The average density of stocking was estimated to be about .9. One of the plots for the yield table study for red spruce carried out by the Northeastern Forest Experiment Station was located in this stand (Meyer, '29). The area was roughly rectangular, with the longer sides facing N. 20° E. and S. 20° W. respectively. The ground cover consisted of at least 60 per cent spruce and fir needles with no living vegetation, about 15 per cent covered by spruce and fir reproduction, mostly about one inch high, and in openings patches of mosses such as *Polytrichum* and *Hylocomium*, making up about 25 per cent of the area. The stand had originated in an old pasture on practically level land. The humus consisted of one inch undecomposed needle litter over a two-inch layer of heavily matted, partially decomposed humus. The mineral soil beneath was a fine, dark brown loam six to eight inches thick with a slight podsol one inch thick at the top. The thinness of the leached horizon points to its formation during the life of the present stand on soil once cultivated. This site was probably once a hardwood ridge, which was early brought into cultivation. Beneath the old cultivated soil was a fine, light brown sand. Logging operations had taken place five or six years before the present observations, making a clean cut on all sides for a distance of at least eight rods from the edges of the stand. Trees on the exposed edges were already beginning to blow down.

METHODS

The observations here reported were made in connection with a survey of reproduction on clear-cut areas in northern New Hampshire, using a wooden frame for laying out milacre (1/1000 acre) quadrats (Baldwin, '27). Such plots were taken at intervals of two rods and all coniferous seedlings were counted on each quadrat, separated by species in one foot height classes. The quadrats were arranged in straight lines run by compass at right angles to the border of the stand from six rods within the forest out into the open. Several strips were run for each exposure, resulting in a total of 63 quadrats as a basis for the analysis.

RESULTS

The tabulated averages for each exposure only are given in order to economize space. The enormous density of small seedlings within the stand is shown graphically by the cross-hatched area in figure 1. The density rapidly diminished with the approach of the cut-over area. Probably only the most firmly rooted seedlings persisted, i.e., those which could resist desiccation of the surface humus. A distinctly denser stocking is shown for the north and east exposures which afforded greater protection from the sun. The excess on these exposures is uniformly too great to be explained entirely by any local condition of soil moisture where the quadrats happened to fall. Probably a

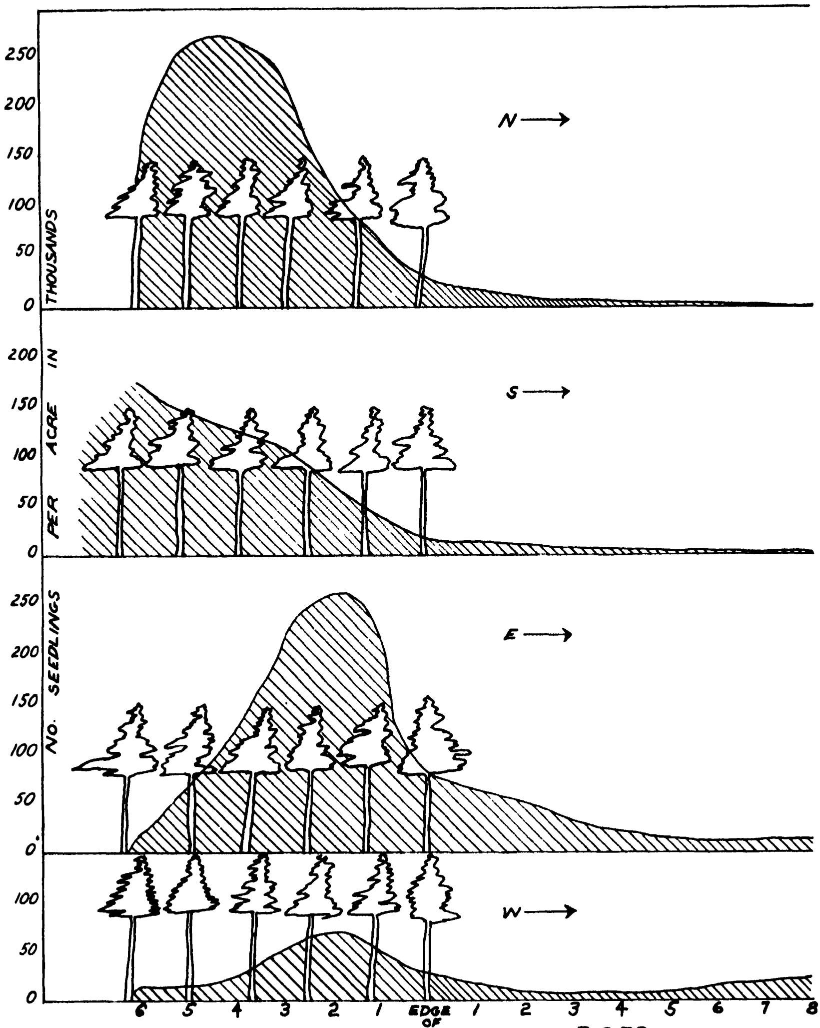

FIG. 1. Diagrammatic representation of the density of reproduction at the edges of a forest stand.

belt transect survey would have given a still better picture of the distribution of reproduction than the method used.

There is much greater variation between west and east than between north and south exposures in this respect. Reproduction is in all cases so ample that the contrasts are less striking.

These observations have been supplemented by others elsewhere in the spruce region. Old pastures serve as excellent examples, and complete clearings of other sorts are less frequent. It appears that Wagner's principle is operative in New England; but reproduction is so abundant and easy to obtain by simple measures that there seems little need for consciously applying it. In the area studied reproduction was indeed satisfactory for full stocking even on the most exposed sides of the stand; in fact a great reduction in density is essential if stagnation is to be avoided. There are many cases, however, where this is not true, and it is well worth keeping in mind that every acre is different, and deserves to be considered on its own merits, and that the principles of natural reproduction, partial shade, protection, conservation of surface soil moisture, and adequate seed supply are applicable everywhere.

TABLE I. *Density of spruce and fir reproduction about a pure stand of red spruce; Dummer, N. H., 1926*

Exposure	Distance from edge of forest rods	Number per acre		
		Balsam	Spruce	Totals
North 20° E				
Forest	6	44,999	89,666	134,665
	4	39,666	242,665	282,331
	2	56,332	74,333	130,665
	Average	46,962	135,554	206,498
Edge of forest		14,666	10,333	24,999
Open	4	1,665	1,998	3,663
	8	999	333	1,332
	Average	1,332	1,165	2,497
South 20° W				
Forest	6	62,666	145,666	208,332
	4	88,333	37,777	126,110
	2	49,332	33,333	82,665
	Average	66,777	72,258	139,035
Edge of forest		9,666	3,666	13,332
Open	4	3,332	666	3,998
	8	1,999	2,332	4,331
	12	2,666	1,000	3,666
	16	2,000	333	2,333
	20	666	1,332	1,998
	Average	2,116	1,132	3,265
South 70° E				
Forest	6	14,666	3,666	18,332
	4	96,999	37,333	134,332
	2	210,999	54,666	265,665
	Average	107,554	31,888	139,443
Edge of forest		40,999	32,999	73,998
Open	4	16,665	7,332	23,997
	8	7,000	3,666	10,666
	Average	11,832	5,499	17,331
North 70° W				
Forest	6	11,999	2,666	14,665
	4	23,333		23,333
	2	52,999	14,000	66,999
	Average	29,443	5,555	34,999
Edge of forest		17,332	8,000	25,332
Open	4	1,999	2,999	4,998
	8	14,998	5,998	20,996
	Average	8,498	4,498	12,997

SUMMARY

Density of spruce and fir reproduction within and outside a pure stand of red spruce was studied by quadrats taken at regular intervals along lines run perpendicular to the edges of the stand.

Reproduction was everywhere very dense, and sufficient for full stocking on all sides. On cut-over land the density of stocking was very much less, due probably to the death by desiccation of small seedlings rooted only in the surface humus.

Reproduction was most abundant on the north and east exposures, corresponding to the greater protection from sun and wind. The density within the stand was least on the west, where possibly the slanting rays of the sun, as well as prevailing winds caused greater heat and drying.

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THE NOMENCLATURE OF PLANT ASSOCIATIONS[1]

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The obvious merits of the Zürich school of plant ecology make it inevitable that its methods and nomenclature shall sooner or later have an American following. It would seem opportune, before all of the faults as well as the virtues of this school shall have been taken over, to criticize the inept and ill-considered nomenclature of plant associations which has been used in certain recent publications. It will be sufficient to draw examples from two works, Braun-Blanquet's " Pflanzensoziologie " (1928) and Rübel's " Pflanzengesellschaften der Erde " (1930).

The former work introduces a nomenclature of plant associations based upon their floristic composition rather than upon their physiognomy. This nomenclature is essentially sound and practical, and there is nothing fundamentally new about it. The floristic point of view is essentially that of folk ecology, and therefore its nomenclature may be traced back to ancient times. Braun-Blanquet's conception of an oak forest is probably the same as that of an intelligent peasant, and he calls it a *quercetum*, as a Roman peasant would have done. The idea of an oak forest is universal, of as great utility to scientists as to peasants, and we may well continue to use the good Latin word *quercetum* as an ecological term. We have inherited the concept and also the word. So far there is no ground for complaint. The difficulty arises when our author wants to be more specific and to express the idea of a particular kind of oak forest, one characterized, let us say, by *Quercus pubescens*. He could be definite and grammatical if he said *quercetum Quercus pubescentis*, but he is so fearful of using more than the minimum number of words with which the idea can possibly be expressed that he says merely *quercetum pubescentis*, which means nothing, since we have a binomial nomenclature in systematic biology. As we shall see, in the further development of his nomenclature he falls more and more into unintelligibility, and finally presents mere jargon for our acceptance.

The basic units to which he wishes to apply names are plant associations such as the oak forest. As we have seen, names exist, or may be coined, following good classical precedent, and in so far as Braun-Blanquet has done this, his names are only to be commended. They are formed on the analogy

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[1] The publication of this article out of the order determined by the receipt of the manuscript has been made possible by funds other than those of the Ecological Society of America.

of *quercetum, salicetum, arboretum, ericetum, fruticetum, graminetum,* etc., good Latin words, of which as many more may be formed as needed, by adding *-etum* to the stem of a substantive noun denoting either a genus or any other definite category of plants.

Such names, however, are generally not sufficiently precise in their application. There are only a few monotypic genera, and in genera which are dominant enough to characterize plant associations the species are usually numerous. Just as it is necessary to have a basically binomial nomenclature (in practice often polynomial) for the units of systematic classification, so the ecologists need a parallel, basically trinomial, nomenclature for associations. It is not enough to designate a sedge meadow as a *caricetum;* it must be designated as a particular kind of a *caricetum,* as for example, one made up predominantly of *Carex curvula.* Nothing could be simpler, it would seem, than to use good Latin and say *caricetum Caricis curvulae*—a sedge association of Carex curvula. If the phrase is a little wordy, there seems to be no help for it. The Zürich ecologists, however, anxious for brevity, meet the difficulty by designating the association made up of *Carex curvula* as a *curvuletum!* The word has no intrinsic meaning, since it is formed from an adjective that occurs in many binomials in many genera. A botanist unacquainted with the European alpine flora would have no possible notion of what a *curvuletum* might be, except from its definition.

If such terms as *curvuletum* are defined and maintained to designate particular associations, it means that we are starting a system of ecological nomenclature that lacks flexibility, that requires the application of rules of priority, that is intrinsically meaningless, and that is made up of terms no better (except for containing a mnemonic) than arbitrary combinations of letters. Do ecologists really want to adopt an arbitrary jargon? Braun-Blanquet's superficial adherence to Latin forms does not make nonsense into sense.

It is only fair to state that Braun-Blanquet also calls his *curvuletum* by the synonym *caricetum curvulae,* a name only slightly less unacceptable. It and all the other names in which the second term of the systematic binomial is used alone, in the genitive case, without a grammatical antecedent, should be condemned as ungrammatical and illogical.

Let us now consider some names that are still worse. We are presented with *molinietum caricetosum Hostianae.* This, if I understand aright, is an association of *Molinia caerulea* containing *Carex Hostiana.* In order to make this guess I have consulted the index of Braun-Blanquet's book and the pages referred to, and have finally gone to the Kew Index and elsewhere to ascertain that there is no *Molinia Hostiana* but that there is a *Carex Hostiana.* Now what does the name really mean? We might infer from *caricetum curvulae,* etc., that the only substantive word in the name would give us a clew to the omitted grammatical antecedent of the genitive adjective. We expect this substantive to have in it the stem of the generic name with which the genitive adjective is to be coupled. But we are wrong. It isn't a *molinietum* of *Molinia Hostiana* at all, for there is no such species. So we assume that it is probably a *molinietum* of the common species *Molinia caerulea,* and proceed to look further at our linguistic monstrosity. We next observe that (grammatically) this *molinietum* is caricetose, *i.e.,* it is full of *cariceta,* associations of *Carex.* As a matter of fact, it is full of *Carex,* not of *cariceta,* and the *Carex* is *Carex Hostiana.* So the puzzle has been solved: "the *Molinia* association full of *Carex* associations of something or other pertaining to Host" turns out to be an association of *Molinia* with *Carex Hostiana.* If we can say this in plain English, or plain German, we can also say it in plain Latin: *molinietum cum Carice Hostiana.*

Another name formed quite similarly to the last would hardly be worth considering if it did not reach a still further height of pedantry and inanity. It is *schoenetum schoenetosum ferruginei*—" a *Schoenus* association filled with *Schoenus* associations, of something-or-other ferrugineous." Actually one finally finds that it is a *schoenetum* distinguished from the typical *schoenetum* of *Schoenus nigricans* by containing also *Schoenus ferrugineus: i.e., schoenetum Schoeni nigricantis et S. ferruginei.* Here we have more words but also more sense.

There is a certain consistency running through Braun-Blanquet's terms which makes one think after a time that he has acquired some facility in guessing what they mean. Then a new vagary turns up. One of them is exemplified by *mesobrometum* and *xerobrometum.* If one did not know that there was no genus *Xerobromus* he might apply what he had learned of Braun-Blanquetian terminology and interpret "*xerobrometum erecti*" as "a *xerobrometum* of *Xerobromus erectus.*" However, it can't be that, and must be "a dry association of *Bromus erectus*" (*i.e., brometum siccum Bromi erecti*).

We are confronted with the name *eleocharetum ovato-atropurpureae.* It is not an association of *Eleocharis ovato-atropurpurea,* for no species, fortunately, bears so outrageous a name, but rather it is an association of *Eleocharis ovata* and *E. atropurpurea.* Such nomenclature embodies false botany as well as bad grammar. Words are the symbols of ideas, and malformed words can only convey garbled ideas.

I have saved until last perhaps the most atrocious of all the names applied to associations. What shall we say of the *trifidi-distichetum?* Is it an association of something trifidly distichous? Just what would such a thing be like? We are given a clue to the puzzle by the statement that the association has *Juncus trifidus* in it. We assume that the "*trifidi*" may refer to this *Juncus,* but our assumption may be wrong. There is no genus *Distichus,* or *Disticha,* or *Distichum,* and so we must assume further that in the flora of the Tatra where this wonderfully named association occurs there is a genus X represented by a species *X distichus,* which perhaps grows with

Juncus trifidus. Is the unknown genus *Sesleria?* If it is, our authors have concealed the fact well.

Braun-Blanquet gives names not only to associations but to groups of associations (Verbände) and groups of Verbände (Ordnungen). The " Verband " has a name derived, in the simplest instances, by adding the suffix *-ion* to the stem (or sometimes a mere fragment) of a generic name. We presume that *-ion* is used as the Greek equivalent of Latin *-ium.* Just why it was considered possible or desirable to bastardize Latin words with a Greek suffix we are not told. It was once jokingly said of a certain botanist whose Latin was more than commonly bad that he thought different case endings were used merely to give words a pleasing diversity, so possibly we have had " -ion " wished upon us, as a new Latin formative, for the sake of achieving a pleasing diversity. Its effect with generic names ending in *-ius, -ia,* or *-ium* is merely to make a hybrid Greek neuter, which has to be declined in Latin in the same way as the corresponding Latin form, and must often, therefore, be indistinguishable in the oblique cases from an unmodified generic name. Quite aside from the general objection to hybrid words, we have here a practical objection to a nomenclature which, if Latin, should be recognizable and intelligible when used in a Latin context. There is still a considerable body of botanical literature currently written in Latin.

Braun-Blanquet sets a bad precedent in forming names of associations and higher categories from mutilated generic names. At any rate, since he discards the physiognomic names of Rübel, we must assume that his *" potamion "* gets its name from *Potamogeton.* Rübel, in taking over Braun-Blanquet's " floristic " system by interpolating it into his own " physiognomic " system, carries mutilation and condensation still farther: witness his *" salherbetum,"* which is not a salt-marsh, as one might at first guess, but an alpine association characterized by *Salix herbacea.* We are informed in a footnote that the derivation of *" salherbetum "* is unmistakable!

The " Ordnung," made up of " Verbände," is designated we are told, by adding to the root of one of the most important association names " the compound suffix *-etalia."* Thus we have *" caricetalia curvulae "* for the " Ordnung " within which the chief " Verband " is the *" caricion curvulae "* and the chief association the *" caricetum curvulae."* This " compound suffix " has the form of a neuter plural. We would get it by adding the neuter adjectival ending *-ale* to the stem of such a substantive as *caricetum* and then making the plural, *e.g., caricetalia* (neuter pl.) from *caricetale* (neuter sing.) Curiously enough, Braun-Blanquet uses *" caricetalia "* as a feminine singular in spite of its neuter plural form. (He writes: " Eine der bestbekannten Ordnungen Mitteleuropas, die subalpin-alpine *Caricetalia curvulae* mässig bis stark saurer, trockener oder frischer Böden, gliedert sich folgendermassen.") Rübel, on the contrary, treats *caricetalia,* correctly, as a plural. (" In der Oekologie unterscheiden sie sich in erster Linie dadurch, dass die *Molinietalia* eine Austrocknung der Bodenoberfläche im Sommer ertragen. . . . Die *Caricetalia fuscae* ertragen eine solche länger andauernde Austrocknung nicht.")

The word "*caricetalia*" is intended to connote "associations related to a *caricetum*." If correctly used, it is not as bad as *caricion,* but of course the binomial *caricetalia curvulae* is open to the same objections as "*caricetum curvulae*."

This singularly bad ecological terminology has hardly as yet been taken up by American botanists, but since an American translation of Braun-Blanquet's book has appeared, it seems timely to point out how thoroughly unsatisfactory it is. Ecology, more than most other branches of biology, seems to have a tendency to run to words rather than to ideas. In view of Braun-Blanquet's sweeping disposal of Clements' ecological nomenclature[2] it cannot be taken amiss if his own proposals meet with equally frank criticism. It is of course realized that some of the ungrammatical, malformed, illogical terms to which he has given currency by taking them up in his "Pflanzensoziologie" may have been devised by other members of the Zürich school. However, the author of a general work which is intended for wide distribution incurs a large responsibility if he does not appraise judiciously what he saves from the quick oblivion of technical periodical literature.

The adoption of Braun-Blanquet's nomenclatorial proposals by Rübel apparently indicates that they have at least the qualified approval of the Zürich school. Although Braun-Blanquet discards entirely the "physiognomic" system of Brockmann-Jerosch and Rübel, together with its terminology, Rübel seems able and quite willing to assimilate the units and nomenclature of the floristic system into his comprehensive physiognomic system. Quite obviously he does not contemplate letting go of his physiognomic terminology, which, as developed originally in collaboration with Brockmann-Jerosch (1912) and retained with minor modifications in the "Pflanzengesellschaften der Erde," presents a long series of Latin names which violate nearly all the principles of word formation. In some respects they are in as conspicuously bad taste as the worst of the "floristic" terms of Braun-Blanquet. Their defects seem to have resulted (1) from a desire to compress into single long compound words ideas that cannot possibly be expressed in respectable Latin without using several words, and (2) from an unfortunate liking for a series of co-ordinate terms with similar endings. The desire to achieve uniformity easily becomes a vice.

There is no reason why there should not be a well considered ecological nomenclature with a combined physiognomic and floristic basis. If it were originally good English, or German, or French, or Spanish, it could easily be translated into Latin for international usage; most successfully if the

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[2] "Clements war es, der die grossen Zusammenhänge in der Vegetationsentwicklung der Erde zu erkennen und in ein System zu bringen versuchte (1916). . . . Uebertriebener Schematismus und eine zungenbrechende Nomenklatur standen indes der Annahme seiner grosszügigen Ideen hinderend im Wege" (p. 263).

task were undertaken by someone with an abhorrence of uniformity. In the past the desire for uniformity and brevity has prevailed over the desire for correct word formation and precision of meaning. A single Latin word is only better than two, or three, or several, when it expresses a concept satisfactorily, with neither perversion of the language nor distortion of the sense. There is much inspiration to be found in the ideas of the Zürich ecologists even if their terminology is unacceptable. It is to be hoped that American ecology will show enough independence to refuse to follow the bad precedents set in the new nomenclature. Braun-Blanquet started with a basically good idea and ended with an exhibition of how badly it could be carried out.

In the literature of American botany, so far, we seem to have only two or three contributions in which the Braun-Blanquet nomenclature, in its least objectionable form, has been adopted. Domin, for example, makes a tentative and unobnoxious trial of it in his "Trinidad and the West Indies" (Totius Orbis Flora Photographica Arte Depicta, Vol. I, 1929), and A. W. Blizzard (Ecology 12: 211, 1931) names a Long Island grassland "*andropogonetum scoparii.*" If we leave out the bamboos, there is almost as much habital diversity within the genus *Andropogon* (in a broad sense) as there is within the whole grass family. Why, therefore, would not *graminetum Andropogonis scoparii* be a scientifically satisfactory as well as grammatical substitute for *andropogonetum scoparii?* This suggestion is thrown out, in closing, to indicate how easily the first step into error may be avoided.

THE DEVELOPMENT OF AN OUT-OF-DOOR BOTANICAL LABORATORY FOR EXPERIMENTAL ECOLOGY[1]

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The idea of an out-of-door laboratory was conceived in response to the need, in the study of ecology, of bringing together the observations made in experimental ecology carried on in a glass laboratory and observations made in the open. This required a laboratory with situations which would make available the plant associations of the surrounding territory and their transitions, and in which further studies could be made upon the plant members and the environmental factors. Such an out-of-door laboratory affords a place in which the results of the in-door laboratory can be checked, by experiment, against those prevailing under natural conditions. It provides a means of projecting the experiments, with modifications, but with a longer duration of time than would be possible in the more limited area under glass. It does, however, make possible the control of a sufficient number of factors to aid in the interpretation of the information acquired in the in-door laboratory. In fact, it makes possible the correlation of facts observed in the glass laboratory with those observed in nature.

President Henry Noble MacCracken and the Board of Trustees of Vassar College accepted this idea and granted to the Department of Botany, in 1920, the use of some four acres of land for this project.

This area (fig. 1) was to be known as The Dutchess County Botanical Garden, and was to be developed with Dutchess County as the basis for ecological study. It has since become popularly known to the students as the Dutchess County Ecological Laboratory. Owing to its proximity to the college buildings, it was necessary to see that this development in no way lessened the aesthetic value of the region, and it was hoped that it might prove that native plants of the county could be used to reclaim waste land, and could blend into an attractive landscape picture.

The project has been of an experimental character, and because the results to date have proven of value in the acquisition of ecological data and the stimulation of interest in ecology, accomplishments thus far are being presented.

The project was to establish, on less than four acres of rough land, the plants native to Dutchess County, N. Y., in their correct associations, with the appropriate environmental factors of each association in this region. In the

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interest of constructive conservation, as well as ecology, it was desired that there should be a study of the natural and artificial methods of propagation of the trees, shrubs and herbaceous forms of the county. With this knowledge at hand, an increased use of native plants may be encouraged with lessened apprehension of their extermination.

An ecological study of the county was necessary before any plans could be made for the use of the area as a laboratory. This study was made in 1921 and 1922, and the report published in pamphlet form in 1923 (Roberts and Shaw, '23). This study gave the ecological, floristic, physiographic and successional information needed as a background for the development of the laboratory.

Fig. 1. The Dutchess County Botanical Garden: A portion of the area as granted.

The four acre plot bordered on the north by the stream, "Fonteyn Kill," offered in several instances locations naturally adapted to the different associations, and advantage was taken of this in the selection of the sites. It was planned to have the associations blend into one another, with as imperceptable a boundary as possible, in order that the transition areas might be given due consideration in their development by the students.

From the beginning, the students made use of the laboratory, and contributed to and cooperated in its development.

In 1922–1923, the Department of Botany was granted the income from the Elizabeth Drinker Storer Fund for seven years, which fund made it possible to proceed with these plans. The situations necessary for the thirty associations found in Dutchess County (table I) were selected in the Dutchess County Botanical Garden (fig. 2), as yet only a rough tract of land, and the land drained as desired.

TABLE I. *Diagrammatic representation of the plant associations in Dutchess County and their successional relations*

I. Upland Succession

1. Open Field Association
↓
2. Open Field Shrub Association
↓
3. Juniper Association
↓
4. Gray Birch Association
↓
5. Pine Association
↓
6. Xerophytic Oak-Hickory Association
↓
7. Mesophytic Oak-Hickory Association
↓
8. Chestnut Association
↓
9. Beech-Maple-Hemlock Association ← 27. Oak-Hickory Association

A. Lake and Pond Series

9. Beech-Maple-Hemlock Association
↑
17. Oak-Hickory Association
↑
(21) 16. Swamp Forest Association
↑
15. Pioneer Swamp Forest Association
↑
14. Swamp Shrub Association
↑
13. Sedge Association
↑
12. Emergent Aquatic Association
↑
11. Floating Aquatic Association
↑
10. Submerged Aquatic Association

B. Bog Series

(21)
↗
20. Bog Forest Association
↑
19. Bog Shrub Association
↑
18. Floating Mat Association

C. River and Stream Series

27. Oak-Hickory Association
↑
26. High Flood Plain Association
↑
25. Low Flood Plain Association
↑
24. Moist Meadow Association
↑
23. Marginal Association
↑
22. Aquatic Association

D. Ravine Series

30. Beech-Maple-Hemlock Ravine Association
↑ ↑
28. Rock Ravine Association
29. Sand Ravine Association

II. Lowland Successions

The entire area on the east, west and south sides was to be bounded by a limestone wall and hedge of arbor vitae. Limestone was chosen because it is much used in the county. This wall (fig. 3) has proven to be most valuable in affording an opportunity for experimenting with the rock plants of all those associations which border on the wall.

The arbor vitae of the open field shrub association makes pleasing green walls to the laboratory, which has the sky for its ceiling.

Paths were planned with the idea of making the locations accessible for the laboratory work of the student and certain consideration was also given to the visitor, who frequents the out-of-door laboratory more often than the in-door one.

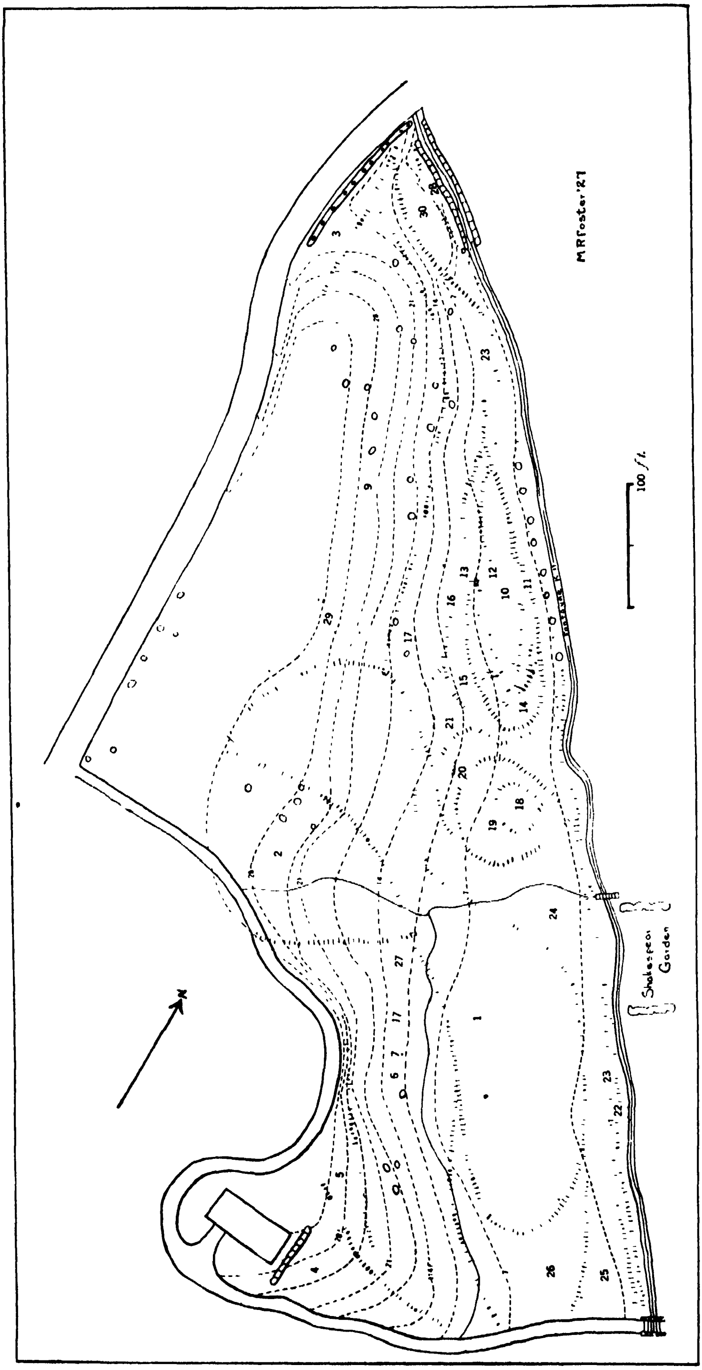


FIG. 2. The Dutchess County Botanical Garden, showing the areas assigned to the thirty associations named in table I. Contour interval 3.5 feet.

Fig. 3. One of the east entrances to the Out-of-door Laboratory, just at the edge of the low flood plain association.

Card No. 1

Botanical Department
Experimental Garden

Taxonomic data

Name Scientific Common
Family Number

Range—County

United States (see map)

Association 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30

Soil reaction

Card No. 2

Botanical Department
Experimental Garden

Morphological Data

Name Scientific Common
Family Number

Habit General Tree Shrub Herb Vine
annual
biennial
perennial

Flower (illustration)
Foliage (illustration)
Fruit
Stem
Root
Duration of effectiveness

Jan. Feb. Mar. Apr. May June Aug. Sept. Oct. Nov. Dec.
Flower
Foliage
Fruit

CARD NO. 3 (front)

BOTANICAL DEPARTMENT
Experimental Garden

Physiological Data

Name Scientific Common
Family Number

Means of Propagation
- Seeds
  - Identification (illustration)
  - Time of collection
  - Time of dispersal
  - Germination (Recommendation)
- Culture of seedling (Recommendation)
- Separation and division
- Layers and runners
- Cuttage
- Buddage and Graftage

CARD NO. 3 (back)

Germination
- External Causes
  - 1. Temperature
  - 2. Moisture
  - 3. Oxygen
  - 4. Light
- Internal Causes
  - a. Seed coat
    - 1. Impervious to water
    - 2. Mechanically resistant
    - 3. Impervious to oxygen
  - b. Embryo
    - 1. Acidity
    - 2. Development
    - 3. Duration of vitality

A water system, by means of surface pipes, with hose connections, was installed, making water available to every part of the laboratory and making it possible to keep the soil moisture factor somewhat under control.

The students in the ecology class of 1923–1924 developed a card system for recording the results of the correlation of their reading, of observations made in the county and of experiments carried on in the in-door and out-of-door laboratories. Copies of these cards are here given.

This same year progress was being made in the establishment of the plants in the streamside association, in the low flood plain association and in the hemlock ravine association.

In September of 1923 Mrs. Opal Davis was given the opportunity of selecting from the many seeds which she had collected for this laboratory, one that would interest her most in a study for her doctor's dissertation. She selected those of *Cornus florida* and started the work upon them at the University of Chicago, completing the study at The Boyce Thompson Institute of Plant Research in 1925 (Davis, '26). In October of 1923, Esther Mitchell, a Vassar College graduate, received a fellowship from The Garden Club of America which enabled her to do research on seed germination with us until 1925. An abstract of the results of her work has been published (Mitchell, '26).

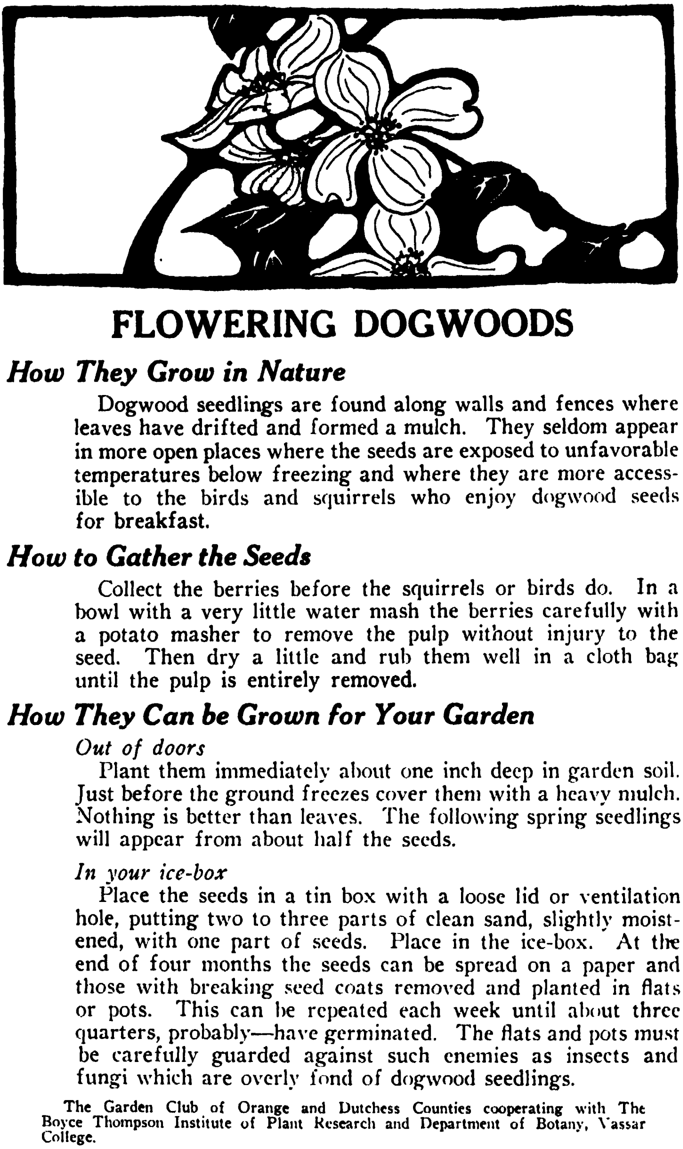
In the interest of conservation and in appreciation of the assistance given by The Garden Club of Orange and Dutchess Counties, the ecology students planned and executed in cooperation with them and The Boyce Thompson Institute of Plant Research, an exhibit at the New York Flower Show in March 1926. The following leaflet (fig. 4) was given out at that time.

Thus the mode of propagation of one of America's attractive shrubs was placed before the general public, and the students themselves realized more keenly, by its immediate utilization, the value of a scientific study. Another study, started in this laboratory, by one of our students, was completed at The University of Washington (Hart, '28).

The book, "American Plants for American Gardens" (Roberts and Rehmann, '29) was based on scientific data, many of which were gained from experiments carried out in this laboratory. The material was presented in a popular manner for the purpose of interesting the general public in constructive conservation and ecological methods.

Each class in ecology has carried forward, through their experiments, the development of the various associations. The very fact that the laboratory gave an opportunity for the recreation of associations has stimulated to a keener and more accurate observation of comparable associations in the field.

Now at the end of ten years, there has been established and may be found in this out-of-door laboratory, of a few acres, the majority of the native plants of Dutchess County growing in their correct associations. It already



FLOWERING DOGWOODS

How They Grow in Nature

Dogwood seedlings are found along walls and fences where leaves have drifted and formed a mulch. They seldom appear in more open places where the seeds are exposed to unfavorable temperatures below freezing and where they are more accessible to the birds and squirrels who enjoy dogwood seeds for breakfast.

How to Gather the Seeds

Collect the berries before the squirrels or birds do. In a bowl with a very little water mash the berries carefully with a potato masher to remove the pulp without injury to the seed. Then dry a little and rub them well in a cloth bag until the pulp is entirely removed.

How They Can be Grown for Your Garden

Out of doors

Plant them immediately about one inch deep in garden soil. Just before the ground freezes cover them with a heavy mulch. Nothing is better than leaves. The following spring seedlings will appear from about half the seeds.

In your ice-box

Place the seeds in a tin box with a loose lid or ventilation hole, putting two to three parts of clean sand, slightly moistened, with one part of seeds. Place in the ice-box. At the end of four months the seeds can be spread on a paper and those with breaking seed coats removed and planted in flats or pots. This can be repeated each week until about three quarters, probably—have germinated. The flats and pots must be carefully guarded against such enemies as insects and fungi which are overly fond of dogwood seedlings.

The Garden Club of Orange and Dutchess Counties cooperating with The Boyce Thompson Institute of Plant Research and Department of Botany, Vassar College.

FIG. 4. A leaflet about the flowering dogwood.

affords to the general public a Botanical Garden in which the opportunity is given for seeing in a limited area, the beauty of many of the native plants of Dutchess County, as it is displayed in natural associations. To the student it offers an out-of-door laboratory in which the principles of ecology may be studied through experiments with the plants of the county.

It is intended to have in each association all the plants in their characteristic grouping and to have some of the plants of each species raised from seeds or spores or vegetatively propagated according to methods known to date. Thus if the public is attracted by the native plants and wishes to use them information will be available for their production. A small nursery, in addition to the general one, has been established in each association, as conditions in these are more comparable to the natural environment of the associations.

Records are being kept of the light, temperature and moisture conditions of air and soil of each association and these, as obtained, are to be compared with those of like associations in the county. These data will be published later.

The status of each association is given in detail below. Since ecology is based upon a study of taxonomy, morphology and physiology, the following presents, under these divisions, some of the outstanding aspects, which have been studied during the development of each association.

In the taxonomic studies emphasis has been placed upon the correct nomenclature[2] of the check list and not upon the monographic or revisional study of plant groups.

In the morphological studies the emphasis is placed upon the adaptation of the structures to the environment of the association and the contribution which the external aspects of the plants offer for landscape work.

In the physiological studies the emphasis is placed mainly upon germination and vegetative propagation experiments, to determine the mode of ecesis of each plant and the methods by which the germination period may be shortened and the plants multiplied for garden use, thereby aiding constructive conservation.

In order to strengthen the ecological phases of the work of the elementary course, a portion (fig. 5), 42 feet by 72 feet, in an undeveloped part of the area assigned to the open field association and low flood plain association was set aside temporarily for an experiment. This portion was bounded by a row of *Cornus alternifolia* L. and a border 9 feet inside this was edged with *Viola cucullata* Ait. Each student was given a 3 foot by 9 foot plot and allowed to carry on certain experiments using only plants of the low flood plain or open field association. The hedge kept this portion from being conspicuous in the laboratory and the violet border unified the plots.

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[2] The ferns are given as in Gray's Manual of 1908. For later work see **Weatherby, C. A.** 1919. Changes in the nomenclature of the Gray's Manual Ferns. *Rhodora,* **21:** 173-179.

FIG. 5. The portion of the garden when used the first year by the beginning students.

In order that the presentation be as brief as possible, certain of the associations, as given in table I, have been combined as indicated:

Upland Series

1. The Open Field Association

(Equivalent of 1 in fig. 2. See figs. 6, 7 and 8.)

a. Taxonomic Studies[3]

HERBS

Achillea millefolium L.	Yarrow
Anaphalis margaritacea (L.) B. & H.	Pearly everlasting
Antennaria neglecta Greene	Everlasting
" *neadioica* Greene	"
" *parlinii* Fernald	"
" *plantaginifolia* (L.) Richards	Plantian-leaved everlasting
Apocynum cannabium L.	Indian hemp
Asclepias amplexicaulis Sm.	Milkweed
" *syriaca* L.	Common milkweed
" *tuberosa* L.	Butterfly weed
Asparagus officinalis L.	Asparagus
Asperula galioides Bieb.	Asperula
Aster cordifolius L.	Aster
" *divaricatus* L.	"
" *ericoides* L.	"
" *laevis* L.	"
" *laterifolius* (L.) B. & H.	"
" *macrophyllus* L.	"
" *novae-angliae* L.	"
" *paniculatus* Lam.	"
" *patens* Ait	"
" *prenanthoides* Muhl.	"
" *ptarmicoides* T. & G.	"
" *vimineus* Lam.	"
Barbarea vulgaris R. Br.	Yellow rocket
Blephilia ciliata (L.) Raf.	Blephilia
Campanula rapunculoides L.	Bellflower
Castilleja coccinea (L.) Spreng.	Scarlet painted cup
Centaurea nigra L.	Spanish buttons
Cerastium vulgatum L.	Common mouse-ear chickweed
" *arvense* L.	Field mouse-ear chickweed
Chrysanthemum leucanthemum L.	Ox-eye daisy
Cichorium intybus L.	Chicory
Cirsium lanceolatum (L.) Hill.	Bull thistle
Convolvulus spithamaeus L.	Bindweed
**Coronilla varia* L.	Coronilla
Corydalis sempervirens (L.) Pers.	Pale corydalis
Cuphea petiolata (L.) Koehne	Clammy cuphea
Daucus carota L.	Carrot

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[3] The names of those plants which are yet to be established in this association in the laboratory are preceded by an asterisk (*). This same method will be followed throughout the paper.

Dianthus armeria L.	Deptford pink
**Dipsacus sylvestris* Huds.	Wild teasel
**Epilobium angustifolium* L.	Fireweed
Erigeron annuus (L.) Pers.	Daisy fleabane
" *philadelphicus* L.	Fleabane
" *pulchellus* Michx.	Robin's plantain
Fragaria virginiana Duchesne	Strawberry
Galium mollugo L.	Bedstraw
Gnaphalium polycephalum Michx.	Common everlasting
" *uliginosum* L.	Low cudweed
Hedeoma pulegioides (L.) Pers.	American pennyroyal
Helianthus divaricatus L.	Sunflower
Hieracium aurantiacum L.	Devil's paint-brush
" *florentinum* All.	King devil weed
* " *gronovii* L.	Hawkweed
" *pilosella* L.	Mouse-ear

FIG. 6. The southeast end of the open field association.

Houstonia caerulea L.	Bluets
Hypericum canadense L.	St. John's-wort
" *perforatum* L.	Common St. John's-wort
Hypoxis hirsuta (L.) Coville	Star grass
Iris versicolor L.	Larger blue flag
Lespedeza capitata Michx.	Bush clover
" *simulata* Mackenzie & Bush	" "
Lilium canadense L.	Wild yellow lily
" *philadelphicum* L.	Wood lily
Linaria vulgaris Hill	Butter and eggs

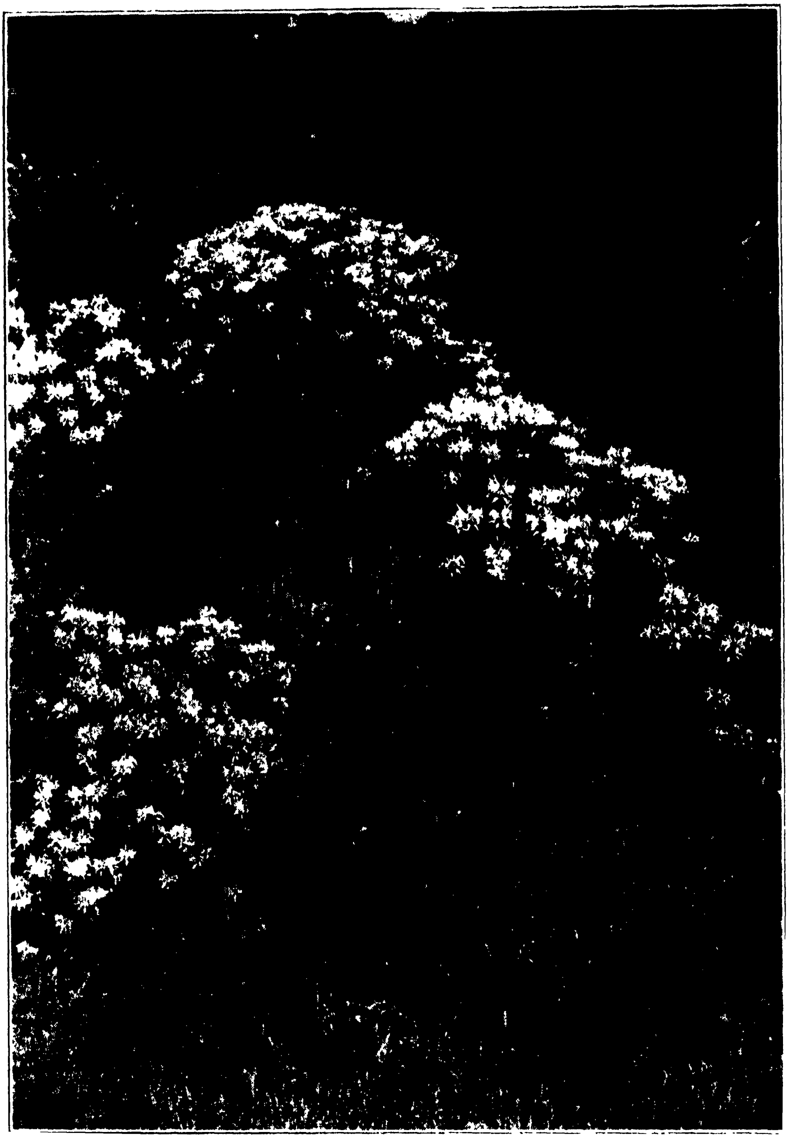

FIG. 7. *Monarda fistulosa* L. established in the southeast end of the open field association.

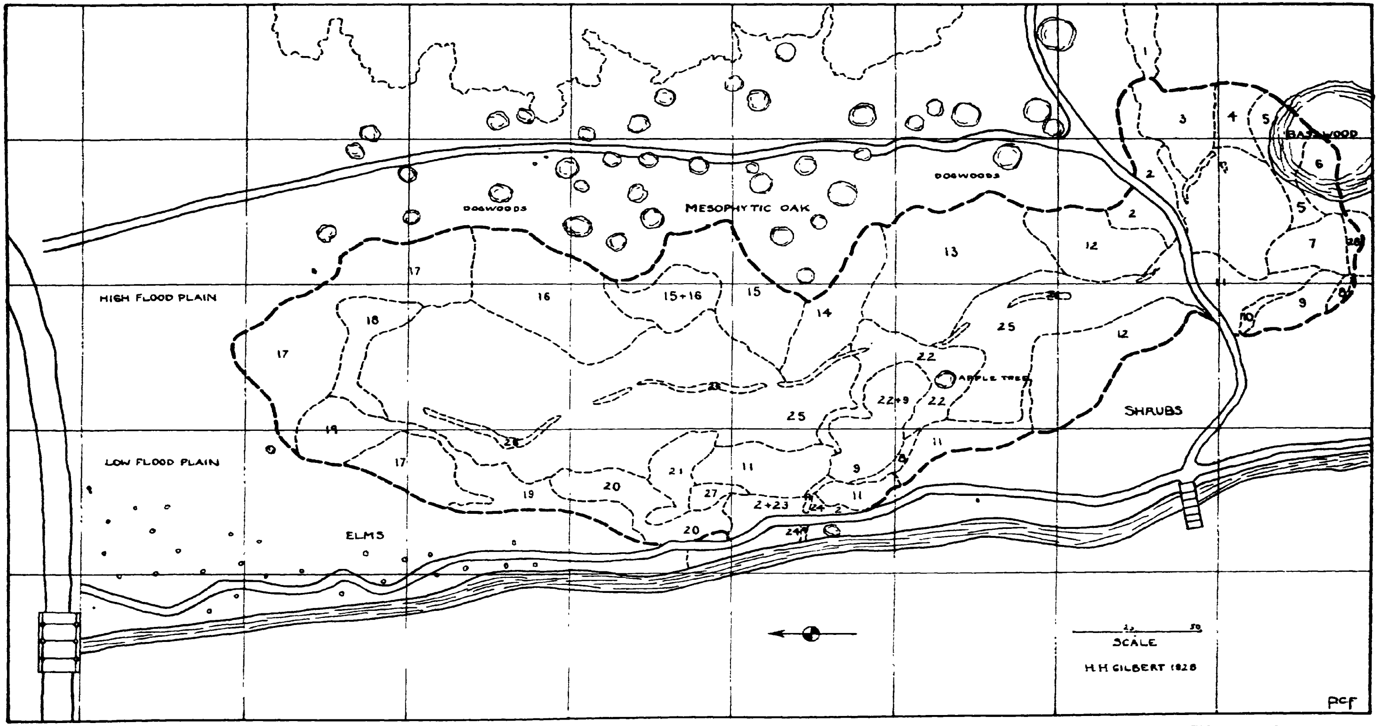

FIG. 8. One of the suggested planting plans made by a student for the open field association. Key to the plan: Figures in parentheses indicate the number planted. 1. *Ceanothus americanus* (5); 2. *Houstonia caerulea;* 3. *Linaria vulgaris;* 4. *Verbascum blattaria;* 5. *Anaphalis margaritacea;* 6. *Podophyllum peltatum;* 7. *Spiraea latifolia* (30); 8. *Lobelia cardinalis* (26); 9. *Iris versicolor* (60); 10. *Iris prismatica* (50); 11. *Aster macrophyllus;* 12. *Dicksonia punctilobula;* 13. *Aster novae-angliae;* 14. *Rudbeckia hirta;* 15. *Lilium philadelphicum* (90); 16. *Lupinus perennis;* 17. *Solidago* (17); 18. *Cichorium intybus;* 19. *Lilium canadense* (90); 20. *Oenothera biennis;* 21. *Hypericum perforatum;* 22. *Ranunculus fascicularis* (20); 23. *Viola fimbriatula;* 24. *Carex* spp.; 25. *Trifolium* spp.; 26. *Asclepias tuberosa* (80); 27. *Asclepias syriaca* (23); 28. *Potentilla fruticosa* (25).

Lobelia inflata L.	Indian tobacco
" *siphilitica* L.	Great lobelia
" *spicata* Lam.	Lobelia
**Lupinus perennis* L.	Wild lupine
Lychnis alba Mill.	White campion
Lysimachia quadrifolia L.	Loosestrife
" *terrestris* (L.) BSP.	"
Medicago falcata L.	Medick
" *sativa* L.	Alfalfa
Melilotus officinalis (L.) Lam.	Yellow melilot
Monarda fistulosa L.	Wild bergamot
Oenothera biennis L.	Common evening primrose
" *fruticosa* L.	Sundrops
" *pumila* L.	Evening primrose
Origanum vulgare L.	Wild marjoram
Opuntia vulgaris Mill.	Prickly pear
Oxalis filipes Small.	Wood sorrel
" *stricta* L.	" "
Pentstemon hirsutus (L.) Willd.	Beard-tongue
Phaseolus polystachyus (L.) BSP.	Wild bean
Physalis pruinosa L.	Strawberry tomato
Phytolacca decandra L.	Common poke berry
Plantago lanceolata L.	Rib grass
" *major* L.	Common plantain
**Polygala sanguinea* L.	Milkwort
" *verticillata* L.	Whorled milkwort
Polygonum virginianum L.	Knotweed
Potentilla arguta Pursh.	Cinquefoil
" *canadensis* L.	"
" *intermedia* L.	"
" *pumila* Poir.	"
" *recta* L.	Rough fruited cinquefoil
Prunella vulgaris L.	Heal-all
Pycnanthemum flexuosum (Wait.) BSP.	Mountain mint
" *virginianum* (L.) Durand & Jackson	" "
Ranunculus bulbosus L.	Bulbous buttercup
" *fascicularis* Muhl.	Early crowfoot
" *septentrionalis* Poir.	Swamp buttercup
Rudbeckia hirta L.	Black-eyed Susan
Rumex acetosella L.	Sheep sorrel
Saponaria officinalis L.	Bouncing bet
Satureja vulgaris (L.) Fritsch	Basil
Silene latifolia (Mill) Britten & Rendle	Bladder campion
" *noctiflora* L.	Night-flowering catchfly
**Sisyrinchium angustifolium* Mill.	Blue-eyed grass
Solanum nigrum L.	Common nightshade
Solidago altissima L.	Golden-rod
" *bicolor* L.	"
" *canadensis* L.	"
" *graminifolia* (L.) Salisb.	"
" *nemoralis* Ait.	"
" *rigida* L.	"
" *rugosa* Mill.	"
" *rugosa* var. *villosa* (Pursh) Fernald	"

Specularia perfoliata (L.) A. DC.	Venus' looking glass
Stachys arenicola Britton	Hedge nettle
Stellaria longifolia Muhl.	Common chickweed
" *media* (L.) Cyrill.	Chickweed
Steironema ciliatum (L.) Raf.	Steironema
Tanacetum vulgare L.	Common tansy
Taraxacum officinale Weber	Common dandelion
Thalictrum polygamum Muhl.	Tall meadow rue
Tragopogon pratensis L.	Goat's beard
Trichostema dichotomum L.	Bastard pennyroyal
Trifolium agrarium L.	Yellow clover
" *arvense* L.	Rabbit-foot clover
" *hybridum* L.	Alsike clover
" *pratense* L.	Red clover
" *procumbens* L.	Low hop clover
" *repens* L.	White clover
Verbascum blattaria L.	Moth mullein
" *thapsus* L.	Common mullein
Verbena urticaefolia L.	White vervain
Veronica officinalis L.	Common speedwell
**Vicia villosa* Roth.	Winter vetch
Viola fimbriatula Sw.	Violet
Waldsteinia fragarioides (Mich.) Trattinick	Barren strawberry

FERNS

Dicksonia punctilobula (Michx.) Gray	Hay-scented fern

b. Morphological Studies

HERBS

Antennaria neglecta Greene
Apocynum androsaemifolium L.
Chrysanthemum leucanthemum L.
Daucus carota L.
Hieracium aurantiacum L.
Oenothera biennis L.
Prunella vulgaris L.
Rumex acetosella L.
Verbascum thapsus L.

c. Physiological Studies

HERBS

Achillea millefolium L.
Anaphalis margaritacea (L.) B. & H.[4]
Anemone virginiana L.[4]
Apocynum cannabinum L.[4]
Asclepias tuberosa L.
Aster cordifolius L.
" *divaricatus* L.
" *ericoides* L.
Cichorium intybus L.
Cuphea petiolata (L.) Koehne
Daucus carota L.[4]
Dianthus armeria L.[4]
Dipsacus sylvestris Huds.
Echium vulgare L.[4]
Hedeoma pulegioides (L.) Pers.
Linaria vulgaris Hill [4]
Lobelia inflata L.
Oenothera biennis L.
Plantago major L.[4]
Potentilla recta L.[4]
" *arguta* Pursh.[4]
Prunella vulgaris L.
Rudbeckia hirta L.
Saponaria officinalis L.[4]

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[4] See Mitchell, '26.

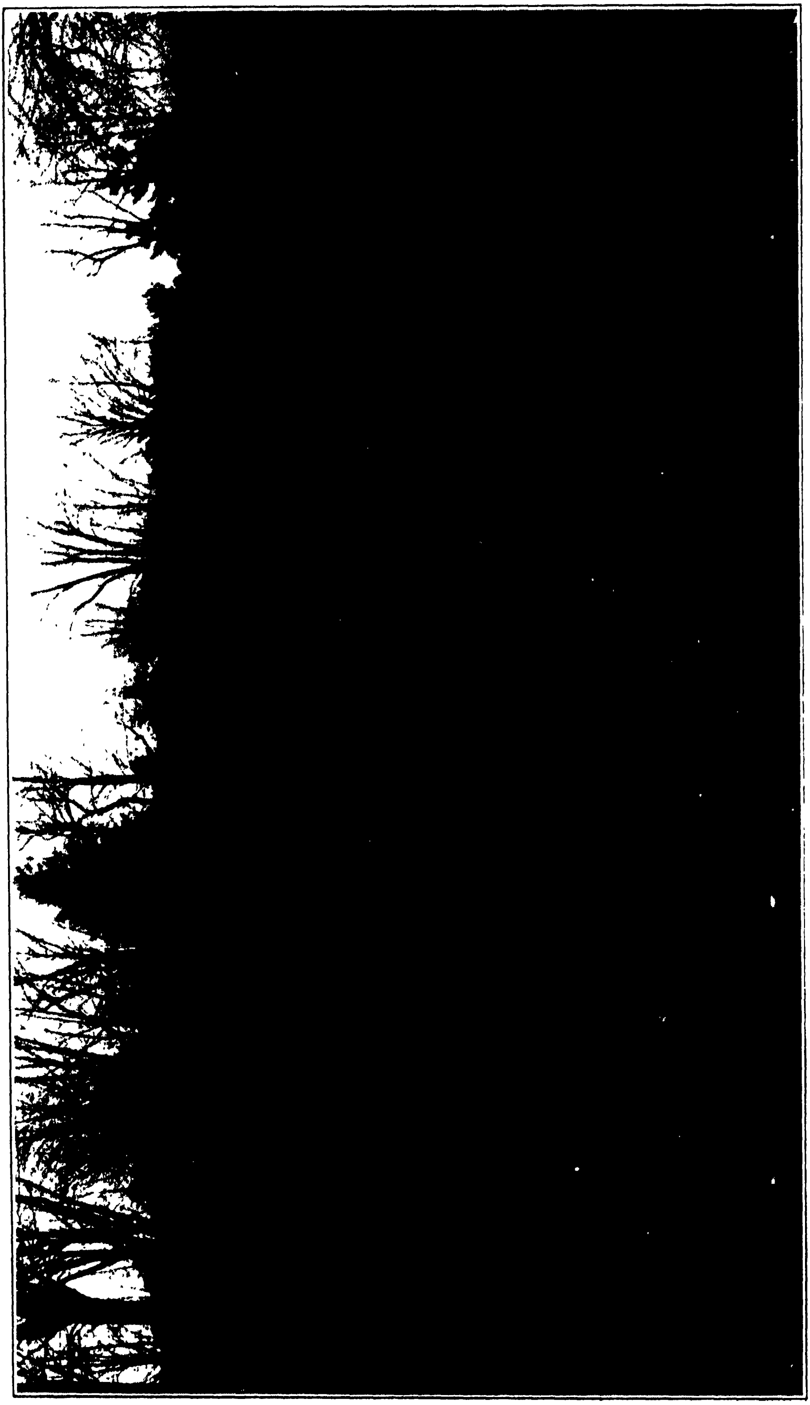

Fig. 9. Open field shrub association with wall and arbor vitae.

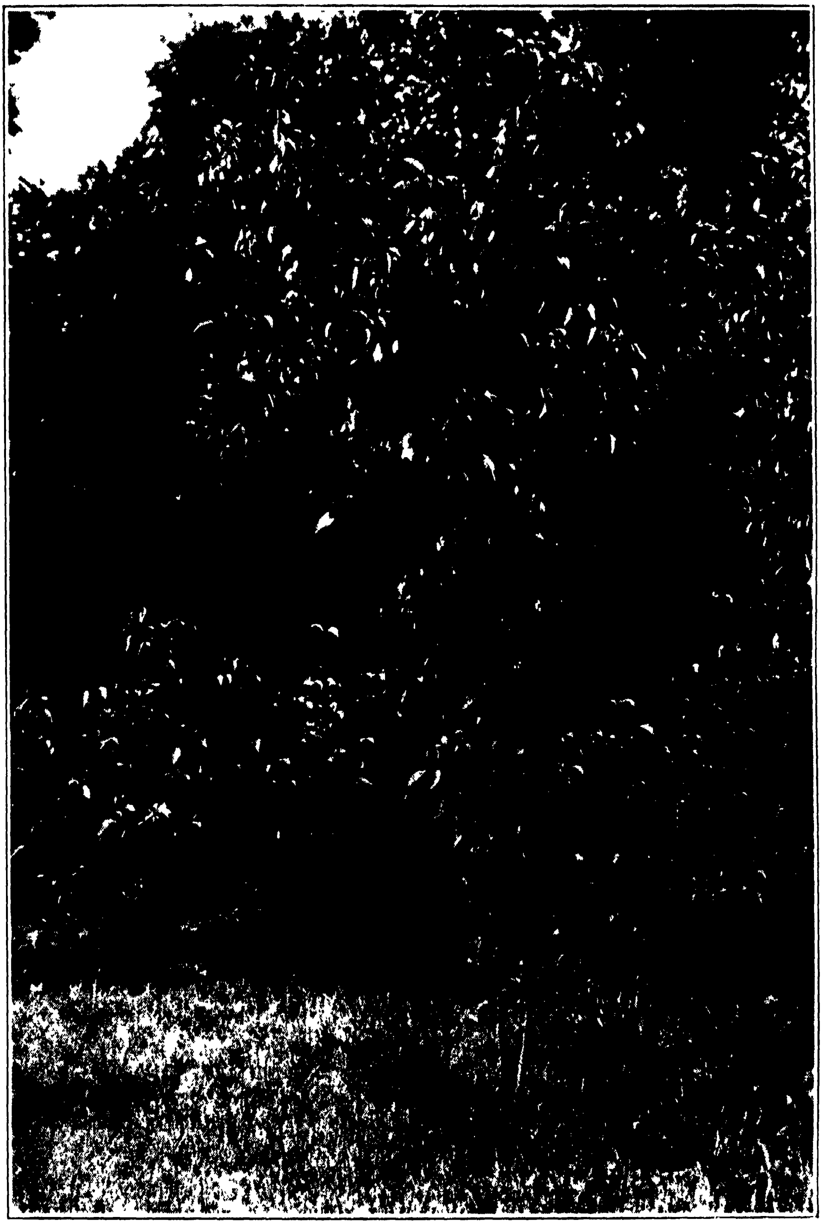

FIG. 10. Open field shrub association in 1932 showing *Staphylea trifolia* L. established.

Silene latifolia (Mill.) Britten and Rendle[4]
Solidago nemoralis Ait.[4]
" *rugosa* Mill.[4]
" *rigida* L.[4]
Tanacetum vulgare L.[4]
Tragopogon pratensis L.
Trifolium agrarium L.
" *arvense* L.
Verbascum blattaria L.[4]
" *thapsus* L.[4]
Verbena urticaefolia L.[4]

FERNS

Dicksonia punctilobula (Michx.) Gray

2. The Open Field Shrub Association

(Equivalent of 2 in fig. 2. See figs. 9 and 10.)

a. Taxonomic Studies

SHRUBS

Celastrus scandens L.	Bitter-sweet
**Cornus circinata* L'Her.	Round-leaved dogwood
" *paniculata* L'Her.	Dogwood
Corylus americana Walt.	Hazelnut
Crataegus sp.	Hawthorn
Juniperus communis L.	Ground juniper
Lonicera sempervirens L.	Trumpet honeysuckle
Lyonia ligustrina (L.) DC.	Male berry
Myrica asplenifolia L.	Sweet fern
Potentilla fructicosa L.	Shrubby cinquefoil
Prunus cuneata Raf.	Plum
" *nigra* Ait.	Canada plum
" *pennsylvanica* L. f.	Pin cherry
" *serotina* Ehrh.	Wild black cherry
" *virginiana* L.	Choke cherry
Psedera quinquefolia (L.) Greene	Virginia creeper
Quercus illicifolia Wang.	Scrub oak
Rhus copallina L.	Dwarf sumach
" *glabra* L.	Smooth sumach
" *typhina* L.	Staghorn sumach
Ribes vulgare Lam.	Red currant
Robinia hispida L.	Rose acacia
Rosa blanda Ait.	Rose
" *rubiginosa* L.	Sweetbrier rose
Rubus allegheniensis Parker	Blackberry
" *idaeus* L.	Raspberry
" *recurvans* Blanchard	Blackberry
" *villosus* Ait.	Dewberry
Spiraea latifolia Borkh.	Meadow-sweet
" *tomentosa* L.	Steeple bush
Viburnum cassinoides L.	Wild raisin
" *dentatum* L.	Arrow-wood
" *lentago* L.	Nannyberry
" *prunifolium* L.	Black haw
* " *pubescens* (Ait.) Pursh	Downy arrow-wood
Vitis aestivalis Michx.	Summer grape
" *labrusca* L.	Northern fox grape
**Zanthoxylum americanum* Mill.	Prickly ash

HERBS

The herbs in the open field shrub association are almost identical with those of the open field association, hence their enumeration is omitted here.

FERNS

Dicksonia punctilobula (Michx.) Gray.

b. Morphological Studies

SHRUBS

Cornus circinata L'Her.

Rosa blanda Ait.

c. Physiological Studies

SHRUBS

Cornus paniculata L'Her
Prunus virginiana L.
Psedera quinquefolia (L.) Greene [1]
Quercus ilicifolia Wang.
Rhus copallina L.[4]
“ *glabra* L.[4]
Rhus typhina L.
Rosa blanda Ait.
“ *rubiginosa* L.
Viburnum lentago L.

3. JUNIPER ASSOCIATION

(Equivalent of 3 in fig. 2. See figs. 11, 12 and 13.)

a. Taxonomic Studies

TREES

Juniperus virginiana L.	Red cedar
Thuja occidentalis L.	Arbor vitae

SHRUBS

Berberis vulgaris L.	Common barberry
Celastrus scandens L.	Bittersweet
Cornus paniculata L'Her.	Dogwood
Juniperus communis L.	Common juniper
Lonicera sempervirens L.	Trumpet honeysuckle
Myrica asplenifolia L.	Sweet fern
* “ *carolinensis* Mill.	Bayberry
Prunus virginiana L.	Choke cherry
Psedera quinquefolia Greene	Virginia creeper
**Quercus ilicifolia* Wang.	Scrub oak
Rhus copallina L.	Dwarf sumach
“ *glabra* L.	Smooth sumach
“ *typhina* L.	Staghorn sumach
**Ribes vulgare* Lam.	Dwarf currant
Rosa blanda Ait.	Rose
“ *rubiginosa* L.	Sweetbrier rose
**Rubus allegheniensis* Porter	Blackberry
* “ *idaeus* L.	Raspberry
* “ *recurvans* Blanchard	Blackberry
“ *villosa* Ait.	Dewberry

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[4] See Mitchell, '26.

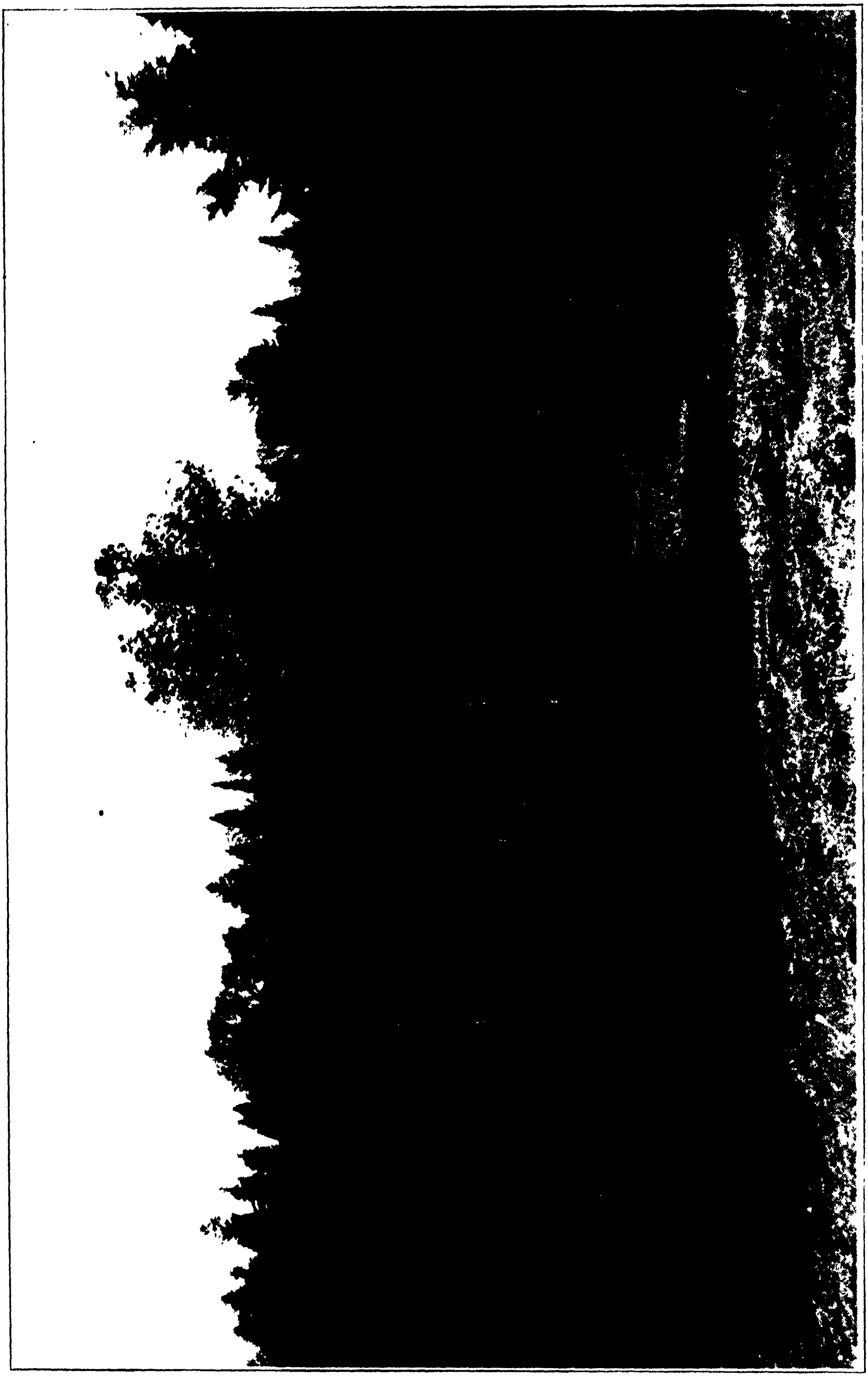

FIG. 11. One of the juniper associations found in Dutchess county.

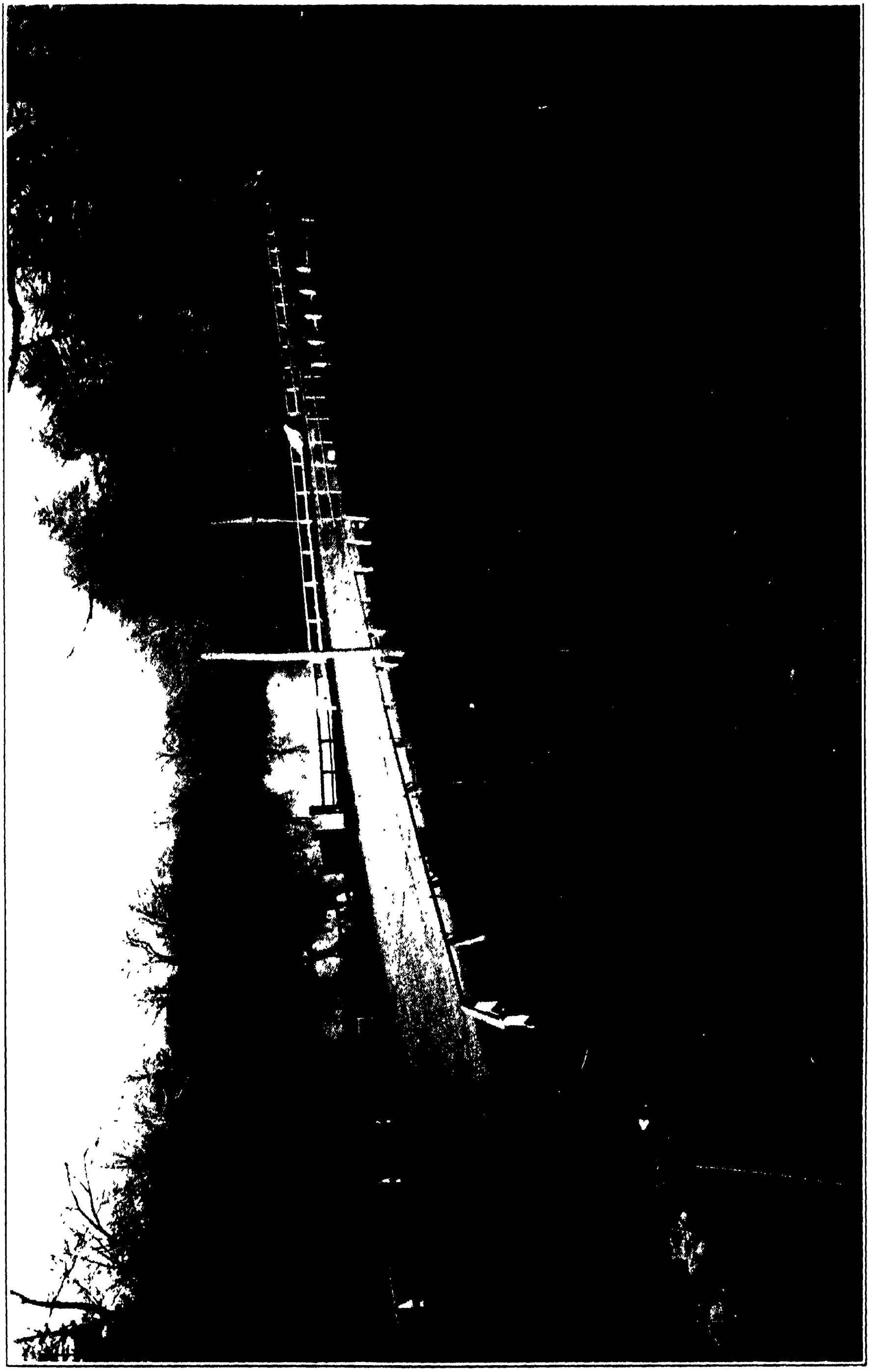

FIG. 12. The beginning of the development of the juniper association in the laboratory in 1925.

FIG. 13. The juniper association in 1932 from the same point as fig. 12.

Vaccinium pennsylvanicum Lam.	Low sweet blueberry
*_Viburnum cassinoides_ L.	Wild raisin
" _dentatum_ L.	Arrow-wood
" _lentago_ L.	Nannyberry
" _prunifolium_ L.	Black haw
* " _pubescens_ (Ait.) Pursh	Downy arrow-wood
Zanthoxylum americanum Mill.	Prickly ash

HERBS

Achillea millefolium L.	Common yarrow
Anaphalis margaritacea (L.) B. & H.	Pearly everlasting
Anemonella thalictroides (L.) Spach	Rue anemone
Antennaria neglecta Greene	Everlasting
" _neodioica_ Greene	"
" _parlinii_ Fernald	"
" _plantaginifolia_ (L.) Richards	Plantain-leaved everlasting
Aquilegia canadensis L.	Wild columbine
Aster cordifolius L.	Aster
" _ericoides_ L.	"
" _novae-angliae_ L.	"
" _prenanthoides_ Muhl.	"
" _vimineus_ Lam.	Small white aster
Blephilia ciliata (L.) Raf.	Blephilia
Cerastium vulgatum L.	Mouse-ear chickweed
*_Chimaphila maculata_ (L.) Pursh	Spotted wintergreen
" _umbellata_ (L.) Nutt.	Pipsissewa
Chrysanthemum leucanthemum L.	Ox-eye daisy
Comandra umbellata (L.) Nutt.	Bastard toad-flax
*_Desmodium nudiflorum_ (L.) DC.	Tick trefoil
Gnaphalium polycephalum Michx.	Cudweed
" _uliginosum_ L.	Low cudweed
Hedeoma pulegioides (L.) Pers.	American pennyroyal
*_Hieracium aurantiacum_ L.	Devil's paint brush
Hypericum canadense L.	St. John's-wort
Lespedeza capitata Michx.	Bush clover
" _simulata_ Mackenzie & Bush	" "
Linaria vulgaris Hill	Butter and eggs
Luzula parviflora (Ehrh.) Desv.	Wood rush
Mitchella repens L.	Partridge berry
Monarda fistulosa L.	Wild bergamot
" _punctata_ L.	Horse mint
Oenothera biennis L.	Common evening primrose
" _fruticosa_ L.	Sundrops
" _pumila_ L.	Evening primrose
Oxalis filipes Small	Wood sorrel
" _stricta_ L.	" "
Plantago lanceolata L.	Rib grass
Polygala paucifiora Willd.	Fringed polygala
Polygonatum biflorum (Walt.) Ell.	Small Solomon's seal
Potentilla argentea L.	Silvery cinquefoil
" _canadensis_ L.	Cinquefoil
" _pumila_ Poir.	"
Prunella vulgaris L.	Self-heal

Pycnanthemum flexuosum (Walt.) BSP.	Mountain mint
* " *virginiana* L.	" "
Pyrola chlorantha Sw.	Shin leaf
" *elliptica* Nutt.	" "
Ranunculus acris L.	Tall buttercup
" *bulbosus* L.	Bulbous buttercup
" *fascicularis* Muhl.	Early crowfoot
Rudbeckia hirta L.	Black-eyed Susan
Saxifraga virginensis Michx.	Early saxifrage
Smilacina racemosa (L.) Desf.	False Solomon's seal
Solidago bicolor L.	Silver-rod
" *graminifolia* (L.) Salisb.	Golden-rod
" *nemoralis* Ait.	"
" *rugosa* Mill.	"
" " var. *villosa* (Pursh) Fernald	Golden-rod
Stellaria media (L.) Cyrill.	Common chickweed
Thalictrum dioicum L.	Early rue
Verbascum blattaria L.	Moth mullein
Veronica officinalis L.	Speedwell
Viola fimbriatula Sm.	Violet
" *latiuscula* Greene	"
" *pubescens* Ait.	"

FERNS

Aspidium marginale (L.) Sw.	Shield fern
Asplenium platyneuron (L.) Oakes	Spleenwort
* " *ruta-muraria* L.	Wall rue
" *trichomanes* L.	Maidenhair spleenwort
Lycopodium obscurum var. *dendroideum* (Michx.) D. C. Eaton	Club-moss
Polypodium vulgare L.	Common polypody
Polystichum acrostichoides (Michx.) Schott.	Christmas fern
Selaginella rupestris (L.) Spring.	

b. Morphological Studies

TREES

Juniperus virginiana L.

SHRUBS

Cornus paniculata L'Her.
Juniperus communis L.
Myrica asplenifolia L.
Viburnum prunifolium L.

HERBS

Aquilegia canadensis L.
Ranunculus bulbosus L.
Veronica officinalis L.

FERNS

Aspidium marginale (L.) Sw.
Camptosorus rhizophyllus (L.) Link.
Polystichum acrostichoides (Michx.) Schott.

c. Physiological Studies

TREES

Juniperus virginiana L.
Thuja occidentalis L.

SHRUBS

Celastrus scandens L.[5]
Cornus paniculata L'Her.
Juniperus communis L.
Myrica asplenifolia L.
Viburnum prunifolium L.[4]

HERBS

Anaphalis margaritacea (L.) B. & H.
Aquilegia canadensis L.

Asplenium platyneuron (L.) Oakes
" *trichomanes* L.
Polypodium vulgare L.
Selaginella rupestris (L.) Spring.
Woodsia obtusa (Spring.) Torr.

FIG. 14. Early stages in the development of the gray birch association.

4. GRAY BIRCH ASSOCIATION

(Equivalent of 4 in fig. 2. See figs. 14, 15, and 16.)

a. Taxonomic Studies

TREES

Betula populifolia Marsh	Gray birch

HERBS

Anaphalis margaritacea (L.) B. & H.	Pearly everlasting
Aster cordifolius L.	Aster
" *prenanthoides* Muhl.	"
" *vimineus* Lam.	"

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[4] See Mitchell, '26.

[5] See Hart, '28.

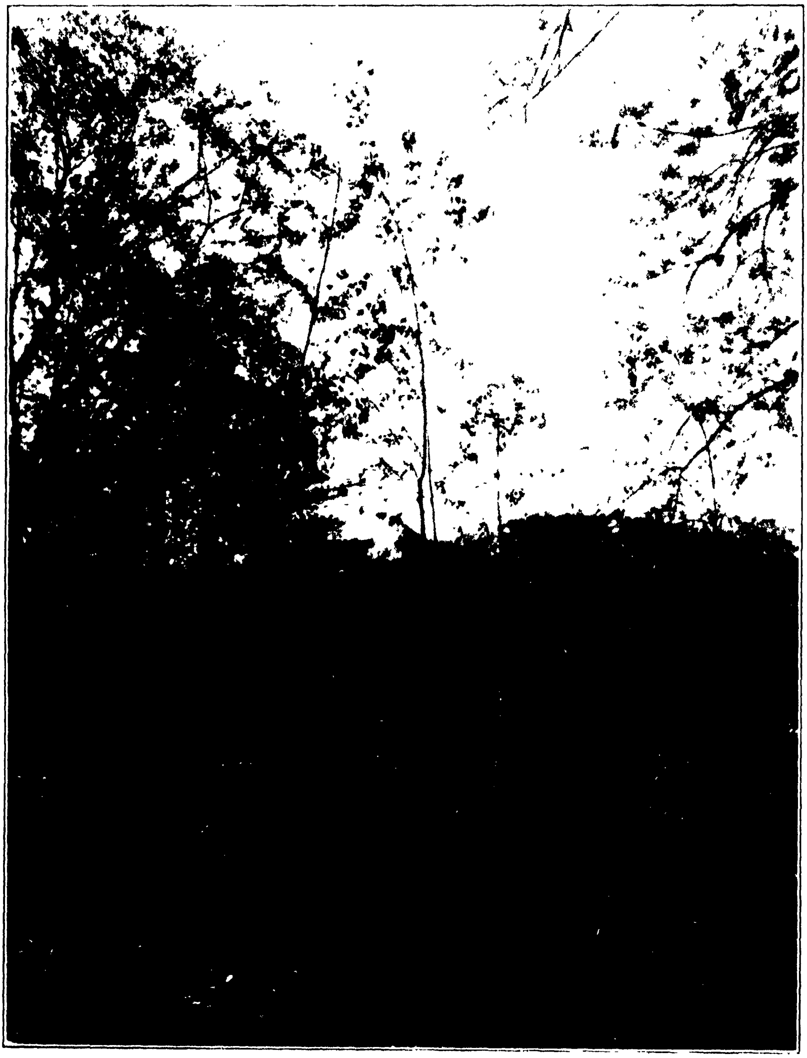
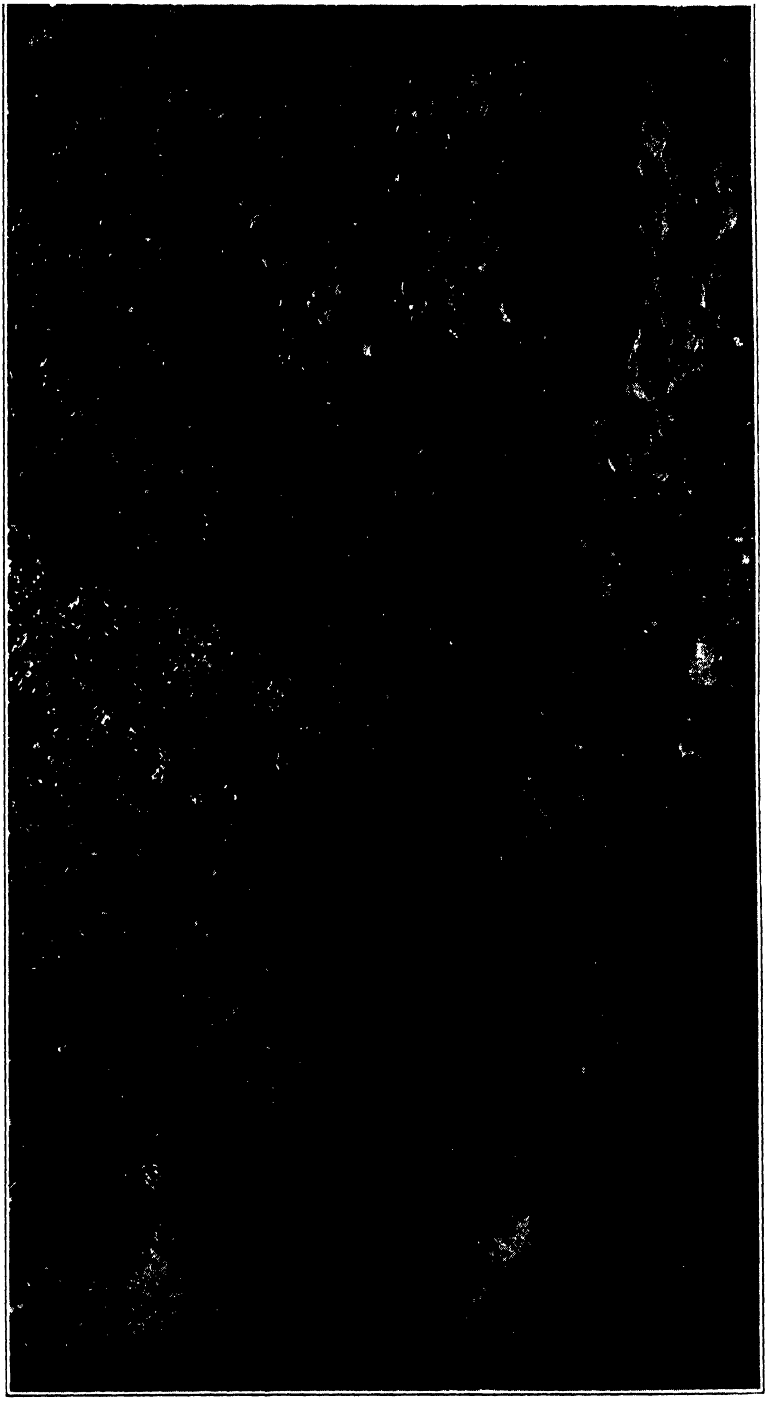


FIG. 15. The gray birch association; an early view from within the laboratory.



F 6. The gray birch association taken from outside the wall of the laboratory in 1931.

Epigaea repens L.	Mayflower
Fragaria virginiana Duchesne	Strawberry
Lespedeza capitata Michx.	Bush clover
" *simulata* Mackenzie & Bush	" "
Oxalis filipes Small	Wood sorrel
" *stricta* L.	" "
Potentilla canadensis L.	Cinquefoil
" *pumila* Poir.	"
Prunella vulgaris L.	Heal-all
Ranunculus acris L.	Tall buttercup
" *bulbosus* L.	Bulbous buttercup
Solidago bicolor L.	Golden-rod
Veronica officinalis L.	Common speedwell

FERNS

Polystichum acrostichoides (Michx.) Schott.

b. Morphological Studies (none)

c. Physiological Studies

TREES

Betula populifolia Marsh

HERBS

Aster prenathoides Muhl.
Aster vimineus Lam.

FIG. 17. Plants of *Lycopodium complanatum* var. *flabelliforme* Fernald, the spores of which are now being used for research studies on their germination and growth.

FERNS

Polystichum acrostichoides (Michx.) Schott.

5. PINE ASSOCIATION

(Equivalent of 5 in fig. 2. See fig. 17.)

a. Taxonomic Studies

TREES

Pinus resinosa Ait.	Red pine
“ *rigida* Mill.	Pitch pine
“ *strobus* L.	White pine

HERBS

**Chimaphila umbellata* (L.) Nutt.	Pipsissewa
Cypripedium acaule Ait.	Stemless lady's slipper
Gaultheria procumbens L.	Checkerberry
Lespedeza capitata Michx.	Bush clover
“ *simulata* Mackenzie & Bush	“ “
Mitchella repens L.	Partridge berry
Pyrola chlorantha Sw.	Shin leaf
“ *elliptica* Nutt.	“ “
Solidago bicolor L.	Silver-rod
“ *canadensis* L.	Golden-rod

FERNS

Aspidium marginale (L.) Sw.	Shield fern
“ *spinulosum* (O. F. Müller) Sw.	Wood fern
Lycopodium clavatum L.	Club moss
“ *obscurum* var. *dendroidium* (Michx.) D. C. Eaton	“ “
Lycopodium complanatum L. var. *flabelliforme* Fernald	Ground pine
Polystichum acrostichoides (Michx.) Schott.	Christmas fern
Scolopendrium vulgare Sm.	Hart's tongue
Selaginella rupestris (L.) Spring.	Selaginella

b. Morphological Studies

HERBS

Mitchella repens L.

c. Physiological Studies

HERBS

Mitchella repens L.[4]

FERNS

Aspidium marginale (L.) Sw.
“ *spinulosum* (O. F. Müller) Sw.
Lycopodium clavatum L.
“ *complanatum* L. var. *flabelliforme* Fernald
Lycopodium obscurum var. *dendroidium* (Michx.) D. C. Eaton
Polystichum acrostichoides (Michx.) Schott.
Scolopendrium vulgare Sm.
Selaginella rupestris (L.) Spring.

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[4] See Mitchell, '26.

6. OAK ASSOCIATION

(Equivalent of 6, 7, 17 and 27 in fig. 2. See figs. 18, 19, 20 and 21.)

a. Taxonomic Studies

TREES

*_Carya alba_ (L.) K. Koch	Mocker nut
“ _glabra_ (Mill.) Spach	Pignut
“ _ovata_ (Mill.) K. Koch	Shagbark hickory
Cornus florida L.	Flowering dogwood
Liriodendron tulipifera L.	Tulip tree
*_Morus alba_ L.	White mulberry
Ostrya virginiana (Mill.) K. Koch	Hop hornbeam
Prunus pennsylvanica L. f.	Wild cherry
“ _serotina_ Ehrh.	“ black cherry
Pyrus americana (Marsh.) DC.	American mountain ash
Quercus alba L.	White oak
* “ _coccinea_ Muench.	Scarlet oak
* “ _muhlenbergii_ Engelm.	Yellow oak
* “ _prinus_ L.	Chestnut oak
“ _rubra_ L.	Red oak
* “ _stellata_ Wang.	Post oak
“ _velutina_ Lam.	Black oak
Sassafras varifolium (Salisb.) Ktze.	Sassafras
Tilia americana L.	Basswood

SHRUBS

Amelanchier canadensis (L.) Medic.	Shad bush
Ceanothus americanus L.	New Jersey tea
Celastrus scandens L.	Bittersweet
Clematis verticillaris DC.	Clematis
Cornus alternifolia L. f.	Alternate-leaved dogwood
Diervilla lonicera Mill.	Bush honeysuckle
*_Gaylussacia frondosa_ (L.) T. & G.	Blue tangle
Hamamelis virginiana L.	Witch-hazel
Ilex verticillata (L.) Gray	Winterberry
Kalmia latifolia L.	Mountain laurel
Lonicera sempervirens L.	Trumpet honeysuckle
Rhamnus cathartica L.	Common buckthorn
Rhododendron nudiflorum (L.) Torr.	Pinxter flower
*_Ribes cynosbati_ L.	Prickly gooseberry
* “ _rotundifolium_ Michx.	Gooseberry
Rosa setigera Michx.	Climbing rose
Rubus odoratus L.	Purple flowering raspberry
Staphylea trifolia L.	Bladdernut
Vaccinium pennsylvanicum Lam.	Low sweet huckleberry
“ _stamineum_ L.	Squaw huckleberry
“ _vacillans_ Kalm.	Late low blueberry
Viburnum acerifolium L.	Arrow-wood
Vitis aestivalis Michx.	Summer grape
“ _labrusca_ L.	Northern fox grape

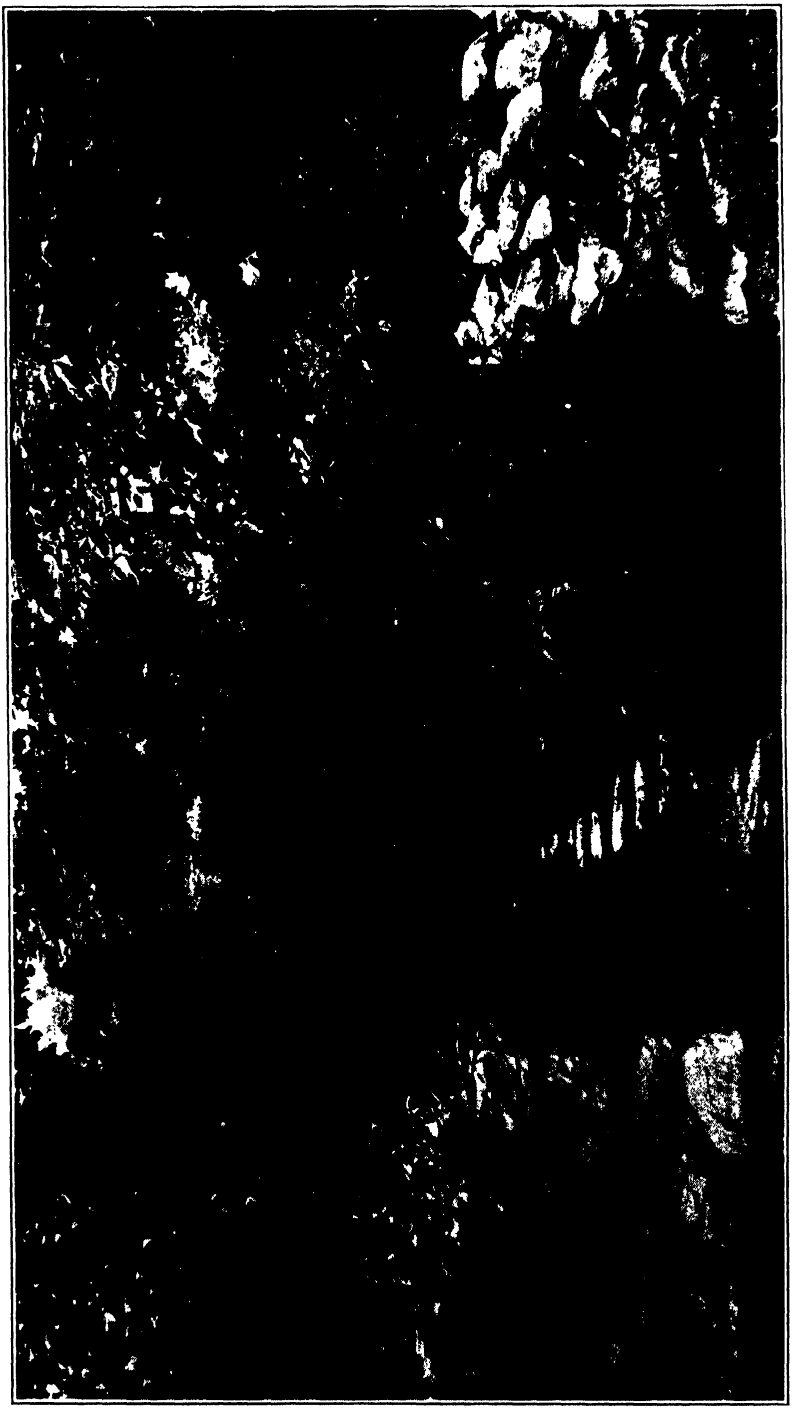

FIG. 18. The southeast entrance of the laboratory in 1931. This path leads directly into the oak association.

FIG. 19. A path in the oak association, bordered by dogwood raised from 1925 seeds germinated in the laboratories of the Boyce-Thompson Institute and Vassar College, Department of Botany.

Fig. 20. A portion of the oak association which is to be developed by the use of the rock plants of this association.

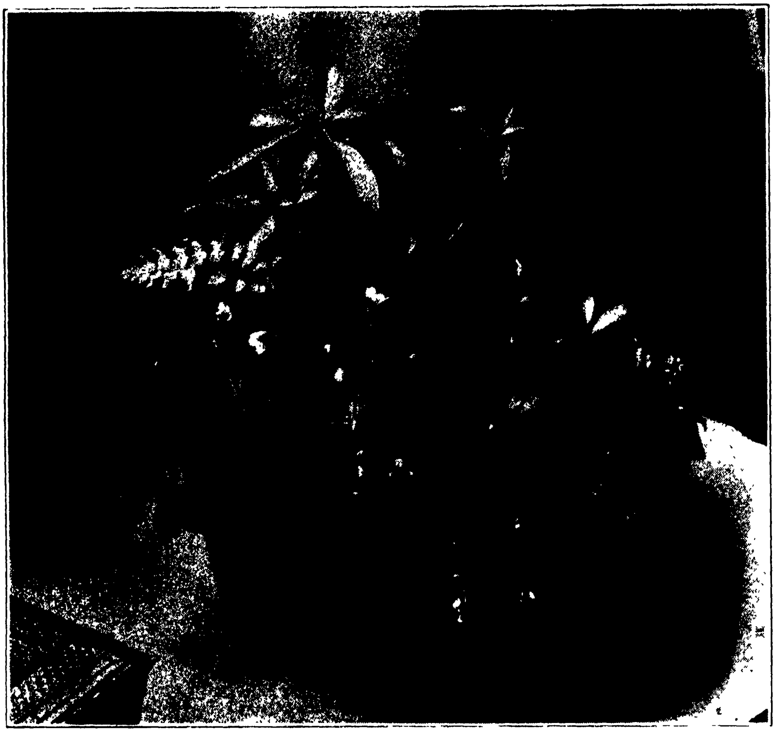

FIG. 21. An interesting by-product of a student's study of the oak association was the creation of it in miniature.

HERBS

Actea alba (L.) Mill.	White baneberry
" *rubra* (Ait.) Willd.	Red baneberry
Anaphalis margaritacea (L.) B. & H.	Pearly everlasting
Anemone quinquefolia L.	Wood anemone
" *virginiana* L.	Anemone
Anemonella thalictroides (L.) Spach	Rue
Antennaria neglecta Greene	Everlasting
" *neodioica* Greene	"
" *plantaginifolia* (L.) Richards	Plantain-leaved everlasting
Aquilegia canadensis L.	Wild columbine
Arabis lyrata L.	Rock cress
Aralia nudicaulis L.	Wild sarsaparilla
Asarum canadense L.	Wild ginger
Asclepias phytolaccoides Pursh.	Poke milkweed
" *quadrifolia* Jacq.	Milkweed
" *variegata* L.	"
Aster acuminatus Michx.	Aster
" *cordifolius* L.	"
" *divaricatus* L.	"
" *infirmus* Michx.	"
" *linarifolius* L.	"
" *macrophyllus* L.	"
" *prenanthoides* Muhl.	"

Baptisia tinctoria (L.) R. Br.	Wild indigo
Chimaphila maculata (L.) Pursh.	Spotted wintergreen
" _umbellata_ (L.) Nutt.	Pipsissewa
Cimicifuga racemosa (L.) Nutt.	Black snakeroot
Claytonia virginica L.	Spring beauty
Comandra umbellata (L.) Nutt.	Bastard toad-flax
Corydalis sempervirens L.	Pale corydalis
*_Cynoglossum virginianum_ L.	Wild comfrey
Cypripedium acaule Ait.	Lady's slipper
Epigaea repens L.	Trailing arbutus
Galium aparine L.	Cleavers
* " _circaezans_ Michx.	Wild licorice
* " _lanceolatum_ Torr.	" "
Gaultheria procumbens L.	Checkerberry
Geranium maculatum L.	Wild cranesbill
Gerardia flava L.	Downy false foxglove
" _virginica_ (L.) BSP.	Smooth false foxglove
Hepatica triloba Chaix.	Hepatica
Heuchera americana L.	Common alum root
Hieracium venosum L.	Poor robin's plantain
*_Hypoxis hirsuta_ (L.) Coville	Star grass
Lespedeza capitata Michx.	Bush clover
" _simulata_ Mackenzie & Bush	" "
Luzula parviflora (Ehrh.) Desv.	Wood rush
Lysimachia quadrifolia L.	Loosestrife
Maianthemum canadense Desf.	Maianthemum
Melampyrum lineare Lam.	Cow wheat
Mitchella repens L.	Partridge berry
Mitella diphylla L.	Bishop's cap
Oakesia sessilifolia (L.) Wats.	Oakesia
Orchis spectabilis L.	Showy orchis
Oxalis filipes Small	Wood sorrel
" _violacea_ L.	Violet wood sorrel
*_Panax trifolium_ L.	Ground nut
Pedicularis canadensis L.	Wood betony
Pentstemon laevigatus Ait. var. _digitalis_ (Sweet) Gray	Beard-tongue
*_Polygala paucifolia_ Willd.	Fringed polygala
Polygonatum biflorum (Walt.) Ell.	Small Solomon's seal
Potentilla canadensis L.	Cinquefoil
" _pumila_ Poir.	"
Prunella vulgaris L.	Self-heal
Pyrola chlorantha Sw.	Shin-leaf
" _elliptica_ Nutt.	"
Sanguinaria canadensis L.	Bloodroot
Saxifraga virginiensis Michx.	Early saxifrage
*_Scrophularia leporella_ Bicknell	Figwort
Smilacina racemosa (L.) Desf.	False spikenard
Solidago bicolor L.	Silver-rod
" _caesia_ L.	Golden-rod
" _latifolia_ L.	"
" _squarrosa_ Muhl.	"
Thalictrum dioicum L.	Early meadow rue
" _revolutum_ DC.	Meadow rue

Tiarella cordifolia L.	Cordifolia
* *Triosteum aurantiacum* Bicknell	Horse gentian
Uvularia grandiflora Sm.	Bellwort
“ *perfoliata* L.	“
Veronica officinalis L.	Speedwell
Viola latiuscula Greene	Violet
“ *palmata* L.	“
“ *pubescens* Ait.	Downy yellow violet
“ *rostrata* Pursh.	Long-spurred violet
“ *triloba* Schwein	Violet

FERNS

Aspidium marginale (L.) Sw.	Shield fern
“ *noveboracense* (L.) Sw.	Wood fern
“ *spinulosum* (O. F. Müller) Sw.	“ “
Asplenium platyneuron (L.) Oakes.	Spleenwort
* “ *ruta-muraria* L.	“
“ *trichomanes* L.	“
Botrychium obliquum var. *dissectum* (Spreng.) Clute	Moonwort
* “ *simplex* E. Hitchcock	“
“ *ternatum* (Thunb.) Sw.	“
“ *virginiana* (L.) Sw.	Rattlesnake fern
Camptosorus rhizophyllus (L.) Link	Walking leaf fern
* *Lycopodium clavatum* L.	Club moss
“ *lucidulum* Michx.	“ “
“ *obscurum* var. *dendroideum* (Michx.) D. C. Eaton	“ “
Pellaea atropurpurea (L.) Link	Cliff brake
Phegopteris hexagonopteris (Michx.) Fée	Beech fern
Polypodium vulgare L.	Polypody
Polystichum acrostichoides (Michx.) Schott.	Christmas fern
“ “ var. *schweinitzii* (Beck) Small	“ “
Pteris aquilina L.	Brake
Woodsia obtusa (Spreng.) Torr.	Woodsia

b. Morphological Studies

SHRUBS

Cornus alternifolia L. f.
Hamamelis virginiana L.
Staphylea trifolia L.
Viburnum acerifolium L.

HERBS

Anemone virginiana L.
Chimaphila umbellata (L.) Nutt.
Epigaea repens L.
Gaultheria procumbens L.
Aster infirmus Michx.
“ *macrophyllus* L.
Gerardia flava L.
Heuchera americana L.[4]
Oakesia sessilifolia (L.) Wats.
Pentstemon laevigatus Ait. var. *digitalis* (Sw.) Gray
Polygonatum biflorum (Walt.) Ell.[4]
Pyrola elliptica Nutt.
Sanguinaria canadensis L.
Smilacina racemosa (L.) Desf.[4]
Saxifraga virginiensis Michx.
Scrophularia leporella Bicknell
Solidago bicolor L.
Smilacina racemosa L. Desf.[4]
Sanguinaria canadensis L.
Saxifraga virginensis Michx.
Triosteum aurantiacum Bicknell

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[4] See Mitchell, '26.

FERNS

Aspidium filix-mas (L.) Sw.
" *marginale* (L.) Sw.
" *noveboracense* (L.) Sw.
Asplenium ruta-muraria L.
Camptosorus rhizophyllus (L.) Link
Pellaea atropurpurea (L.) Link
Phegopteris hexagonopteris (Michx.) Fée
Woodsia obtusa (Spreng.) Torr.

c. Physiological Studies

TREES

Prunus serotina Ehrh.
Tilia americana L.

SHRUBS

Ceanothus americanus L.
Cornus alternifolia L. f.
Hamamelis virginiana L.
Staphylea trifolia L.
Rhamnus cathartica L.
Viburnum acerifolium L.[4]

HERBS

Anemone virginiana L.
Asarum canadense L.
Aster divaricatus L.

7. Beech-Maple-Hemlock Association

(Equivalent of 9 in fig. 2. See fig. 22.)

a. Taxonomic Studies

TREES

Acer pennsylvanicum L.	Striped maple
Acer saccharum Marsh.	Sugar maple
" *spicatum* L.	Mountain maple
Betula alba L.	White birch
" *lenta* L.	Black birth
" *lutea* Michx.	Yellow birch
**Castanea dentata* (Marsh.) Borkh.	Chestnut
Cornus florida L.	Flowering dogwood
Fagus grandifolia Ehrh.	Beech
Fraxinus americana L.	White ash
Liriodendron tulipifera L.	Tulip tree
Tilia americana L.	Basswood
Tsuga canadensis (L.) Carr.	Hemlock

SHRUBS

Amelanchier canadensis (L.) Medic.	Shad bush
" *oblongifolia* (T. & G.) Roem.	Juneberry
Cornus alternifolia L. f.	Alternate-leaved dogwood
Hamamelis virginiana L.	Witch-hazel
Kalmia latifolia L.	Mountain laurel
Taxus canadensis Marsh.	American yew
Viburnum acerifolium L.	Arrow-wood
" *lantana* L.	Wayfaring tree

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[4] See Mitchell, '26.

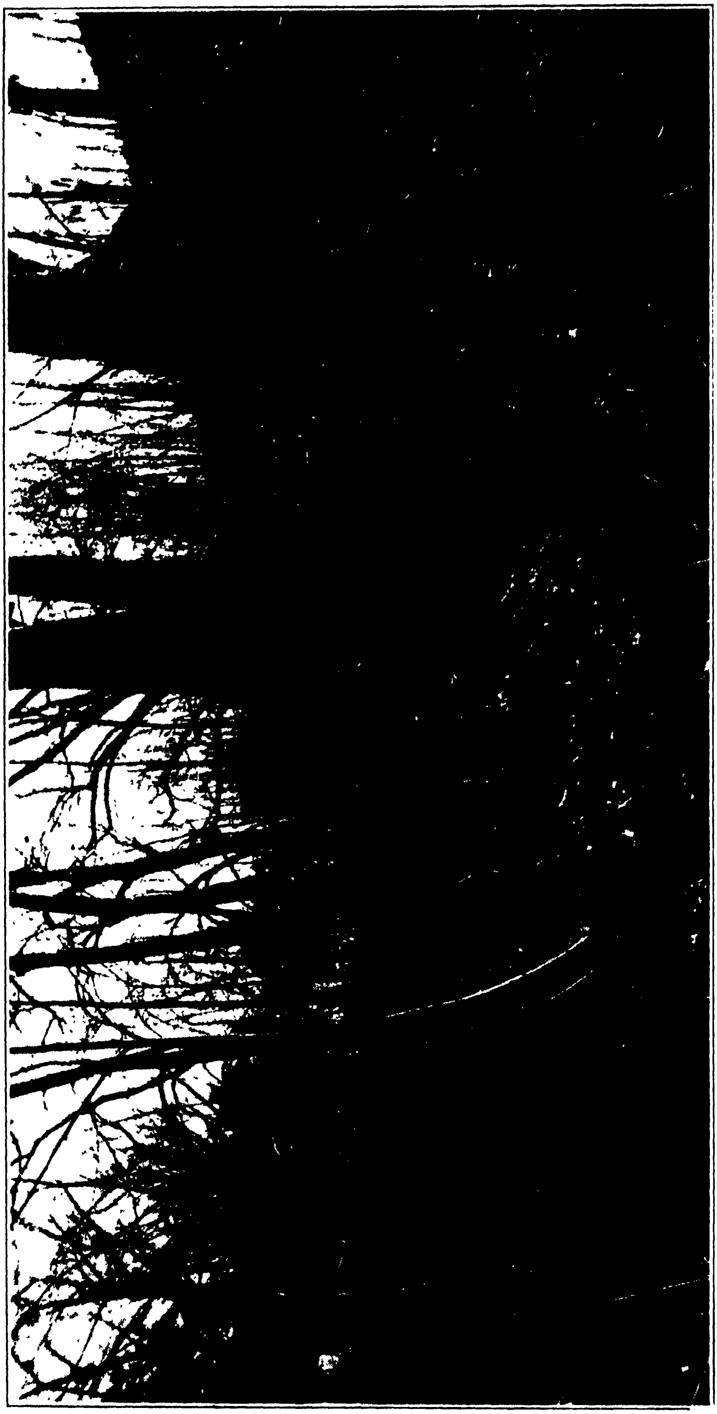

FIG. 22. A portion of the beech-maple-hemlock association, selected because of the two existing old hard maple trees.

HERBS

Actea alba (L.) Mill.	White baneberry
" _rubra_ (Ait.) Willd.	Red baneberry
Asarum canadense L.	Wild ginger
*_Circaea lutetiana_ L.	Enchanter's nightshade
Cornus canadensis L.	Bunchberry
Cypripedium acaule Ait.	Stemless lady's slipper
Dicentra cucullaria (L.) Bernh.	Dutchman's breeches
Epifagus virginiana (L.) Bart.	Beech-drops
*_Eupatorium urticaefolium_ Reichard.	White snakeroot
Geranium robertianum L.	Herb Robert
Heuchera americana L.	Common alum root
Luzula parviflora (Ehrh.) Desv.	Wood rush
Maianthemum canadense Desf.	Maianthemum
Medeola virginiana L.	Indian cucumber-root
Mitchella repens L.	Partridge berry
Mitella diphylla L.	Bishop's cap
Monotropa uniflora L.	Indian pipe
Orchis spectabilis L.	Showy orchis
Oxalis acetosella L.	Common wood sorrel
" _violacea_ L.	Violet wood sorrel
Polygonatum biflorum (Walt.) Ell.	Small Solomon's seal
*_Prenanthes alba_ L.	White lettuce
" _trifoliata_ (Cass.) Fernald	Gall-of-the-earth
Smilacina racemosa (L.) Desf.	False spikenard
Streptopus roseus Michx.	Twisted-stalk
Tiarella cordifolia L.	False miterwort
Trientalis americana (Pers.) Pursh	Star flower
Trillium erectum L.	Wake robin
" _grandiflorum_ (Michx.) Salisb.	" "
Uvularia grandiflora Sm.	Bellwort
" _perfoliata_ L.	"
Viola blanda Willd.	Violet
" _palmata_ L.	"
" _pubescens_ Ait.	Downy yellow violet
" _rostrata_ Pursh	Long-spurred violet
" _sororia_ Willd.	Violet
" _triloba_ Schwein.	"

FERNS

Adiantum pedatum L.	Maidenhair fern
Aspidium marginale (L.) Sw.	Shield fern
" _noveboracense_ (L.) Sw.	Wood fern
" _spinulosum_ (O. F. Müller) Sw.	" "
Asplenium filix-femina (L.) Beenh.	Lady fern
" _platyneuron_ (L.) Oakes	Spleenwort
* " _ruta-muraria_ L.	"
" _trichomanes_ L.	"
Botrychium obliquum var. _dissectum_ (Spreng.) Clute	Moonwort
" _ternatum_ (Thunb.) Sw.	"
" _virginianum_ (L.) Sw.	Rattlesnake fern

Camptosorus rhizophyllus (L.) Link.	Walking leaf
Cystopteris fragilis (L.) Bernh.	Bladder fern
Dicksonia punctilobula (Michx.) Gray	Hay-scented fern
Pellaea atropurpurea (L.) Link.	Cliff brake
Phegopteris dryopteris (L.) Fée	Oak fern
“ *hexagonoptera* (Michx.) Fée	Beech fern
“ *polypodioides* Fée	“ “
Polypodium vulgare L.	Polypody
Polystichum acrostichoides (Michx.) Schott	Christmas fern
Woodsia obtusa (Spreng.) Torr.	Woodsia

b. Morphological Studies (none)

c. Physiological Studies

TREES

Cornus florida L.

HERBS

Cypripedium acaule Ait.
Mitella diphylla L.
Prenanthes trifoliata (Cass.) Fernald

FERNS

Adiantum pedatum L.
Asplenium acrostichoides Sw.
Cryptogramma stelleri (Gme.) Prantl.
Cystopteris fragilis (L.) Berch.
Dicksonia punctilobula (Michx.) Gray
Phegopteris polypodioides Fée
Polystichum acrostichoides (Michx.) Schott.

Lowland Series

8. LAKE AND POND ASSOCIATION

(Equivalent of 10, 11, 12, 13, 14, 15 and 16 in fig. 2. See figs. 23 and 24.)

a. Taxonomic Studies

TREES

Acer rubrum L.	Red maple
**Nyssa sylvatica* Marsh.	Sour gum
**Quercus palustris* Muench.	Pin oak
Salix nigra Marsh.	Black willow

SHRUBS

Alnus incana (L.) Moench.	Hoary alder
“ *rugosa* (Du Roi) Spreng.	Smooth alder
Benzoin aestivale (L.) Nees	Spice bush
Cephalanthus occidentalis L.	Buttonbush
Clematis virginiana L.	Clematis
Clethra alnifolia L.	Sweet pepperbush
Cornus amomum Mill.	Kinnikinnik
“ *stolonifera* Michx.	Red-osier dogwood
Crataegus crus-galli L.	Hawthorn
* “ *fecunda* Sarg.	“
Gaylussacia baccata (Wang.) C. Koch	Black huckleberry
“ *dumosa* (Andr.) T. & G.	Dwarf huckleberry
**Ilex laevigata* (Pursh) Gray	Smooth winterberry
“ *verticillata* (L.) Gray	Winterberry
**Myrica gale* L.	Sweet gale

Potentilla fruticosa L.	Shrubby cinquefoil
Pyrus arbutifolia (L.) L. f. var. *atropurpurea* (Britt.) Rob.	Chokeberry
* *Pyrus melanocarpa* (Michx.) Willd.	"
* *Quercus ilicifolia* Wang.	Black scrub oak
Rhododendron viscosum (L.) Torr.	Clammy Azalea
* *Ribes oxyacanthoides* L. var. *calcicola* Fernald	Smooth gooseberry
Rosa carolina L.	Rose
" *nitida* Willd.	"
" *virginiana* Mill.	"

Fig. 23. The pond association at the time of excavation. It has a natural clay bottom and is fed by springs from the hillside.

* *Rubus hispidus* L.	Blackberry
* *Salix balsamifera* Barratt.	Willow
" *candida* Flügge	Hoary willow
" *cordata* Muhl.	Willow
" *discolor* Muhl.	Glaucous willow
" *glaucophylla* Bebb.	Willow
" *lucida* Muhl.	Shining willow
* " *petiolaris* Sm.	Willow
* " *sericea* Marsh.	Silky willow
* " *serissima* (Bailey) Fernald	Autumn willow
Sambucus canadensis L.	Common alder

**Smilax herbacea* L.	Carrion-flower
" *rotundifolia* L.	Common green brier
Solanum dulcamara L.	Climbing nightshade
Spiraea latifolia Borkh.	Meadow-sweet
" *tomentosa* L.	Steeple bush
Vaccinium corymbosum L.	High blueberry
Viburnum dentatum L.	Arrow-wood

FIG. 24. An edge of the pond association in 1931.

HERBS

Acorus calamus L.	Sweet flag
Alisma plantago-aquatica L.	Water plantain
Arisaema triphyllum (L.) Schott.	Jack-in-the-pulpit
Asclepias incarnata L.	Swamp milkweed
Aster lateriflorus (L.) Britt.	Aster
" *novae-angliae* L.	"
" *paniculatus* Lam.	"
" *puniceus* L.	"
" *vimineus* Lam.	"
Barbarea vulgaris R. Br.	Yellow rocket
Brasenia schreberi Gmel.	Water shield
Caltha palustris L.	Marsh marigold
Campanula aparinoides Pursh.	" bluebell

Castalia odorata (Ait.) Woodville & Wood.	Sweet-scented water lily
Cerastium nutans Raf.	Chickweed
Ceratophyllum demersum L.	Hornwort
Chelone glabra L.	Turtlehead
Chrysosplenium americanum Schwein.	Golden saxifrage
Cicuta bulbifera L.	Water hemlock
* " *maculata* L.	Spotted cowbane
Conioselinum chinense (L.) BSP.	Hemlock parsley
Elodea canadensis Michx.	Water-weed
Epilobium molle Torr.	Willow-herb
Eriocaulon articulatum (Huds.) Morong.	Pipewort
Eriophorum gracile Roth.	Cotton grass
Eupatorium perfoliatum L.	Boneset
" *purpureum* L.	Joe-Pye weed
Gentiana andrewsii Griseb.	Closed gentian
" *crinita* Froel.	Fringed gentian
Helenium autumnale L.	Sneezeweed
Heracleum lanatum Michx.	Cow parsnip
Hydrocotyle americana L.	Water pennywort
Hypericum boreale (Britt.) Bicknell	St. John's-wort
" *punctatum* Lam.	"
" *virginicum* L.	Marsh wort
**Iris prismatica* Pursh.	Slender blue flag
" *versicolor* L.	Larger blue flag
Juncus effusus L.	Common rush
* " *marginatus* Rost.	Rush
Lemna minor L.	Duckweed
* " *trisulca* L.	"
Lobelia cardinalis L.	Cardinal flower
* " *siphilitica* L.	Great lobelia
**Ludvigia alternifolia* L.	Seedbox
Lycopus virginicus L.	Bugle weed
Lysimachia nummularia L.	Moneywort
" *producta* (Gray) Fernald	Loosestrife
Lythrum alatum Pursh.	"
**Mikania scandens* (L.) Willd.	Climbing hemp-weed
Mimulus ringens L.	Monkey flower
Myosotis laxa Lehm.	Forget-me-not
Myriophyllum farwellii Morong.	Water milfoil
" *spicatum* L.	" "
**Najas flexilis* (Willd.) Rostk. & Schmidt.	Naiad
Nymphaea advena Ait.	Yellow pond lily
Orontium aquaticum L.	Golden club
Peltandra virginica (L.) Kunth	Arrow arum
Penthorum sedoides L.	Ditch stonecrop
Polygonum acre HBK.	Water smartweed
" *amphibium* L.	Knotweed
" *arifolium* L.	Halbert-leaved tear-thumb
* " *hydropiper* L.	Common smartweed
" *muhlenbergii* (Meisn.) Wats.	Knotweed
" *pennsylvanicum* L.	"
* " *persicaria* L.	Lady's thumb
" *sagittatum* L.	Arrow-leaved tear-thumb

Pontederia cordata L.	Pickerel-weed
* *Potamogeton alpinus* Balbis	Pondweed
" *americanus* C. & S.	"
" *heterophyllus* Schreb.	"
* " *hillii* Morong.	"
" *lucens* L.	"
* " *natans* L.	"
* " *pectinatus* L.	"
" *perfoliatus* L.	"
* " *robinsii* Oakes	"
* " *zosterifolius* Schumacher	"
Potentilla palustris (L.) Scop.	Marsh five-finger
Proserpinaca palustris L.	Mermaid-weed
Radicula aquatica (Eat.) Robinson	Lake cress
Ranunculus abortivus L.	Small-flowered crowfoot
" *aquaticus* L. var *capillaceus* DC.	Common white water crowfoot
" *circinatus* Sibth.	Stiff water crowfoot
" *delphinifolius* Torr.	Yellow water crowfoot
" *recurvatus* Poir.	Hooked buttercup
" *septentrionalis* Poir.	Swamp buttercup
Sagittaria latifolia Willd.	Arrow-head
Saxifraga pennsylvanica L.	Swamp saxifrage
Scutellaria galericulata L.	Scullcap
" *lateriflora* L.	Mad-dog skullcap
Senecio aureus L.	Golden ragwort
Solidago elliotii T. & G.	Golden-rod
Sparganium americanum Nutt.	Bur-reed
" " var. *androcladum* (Engelm.) Fernald & Eames	"
* *Sparganium eurycarpum* Engelm.	"
* " *lucidum* Fernald & Eames	"
* " *minimum* Fries	"
Spirodela polyrhiza (L.) Schleid.	Duckweed
Symplocarpus foetidus (L.) Nutt.	Skunk cabbage
Thalictrum polygamum Muhl.	Tall meadow rue
Thaspium aureum Nutt.	Meadow parsnip
* *Typha angustifolia* L.	Cat-tail
" *latifolia* L.	"
Utricularia minor L.	Smaller bladderwort
" *vulgaris* L.	Greater bladderwort
Vallisneria spiralis L.	Tape grass
Verbena hastata L.	Blue vervain
" *urticaefolia* L.	White vervain
Vernonia noveboracensis Willd.	Ironweed
Veronica serpyllifolia L.	Thyme-leaved speedwell
Viola conspersa Reichenb.	Violet
" *cucullata* Ait.	"
" *pallens* (Banks.) Brainerd	Sweet white violet
" *papilonacea* Pursh.	Violet
" *sororia* Willd.	"
Wolffia columbiana Karst.	Wolffia

FERNS

Aspidium cristatum (L.) Sw.	Shield fern
" *thelypteris* (L.) Sw.	Wood fern
Equisetum palustre L.	Horsetail
Onoclea sensibilis L.	Sensitive fern
Osmunda cinnamomea L.	Cinnamon fern
" *claytoniana* L.	Flowering fern
" *regalis* L.	" "
Selaginella apus (L.) Spring.	Selaginella
Woodwardia virginica (L.) Sm.	Chain fern

b. Morphological Studies

SHRUBS

Pyrus arbutifolia (L.) L. f.

c. Physiological Studies

SHRUBS

Alnus incana (L.) Moench.
Benzoin aestivale (L.) Nees
Cephalanthus occidentalis L.
Cornus amomum Mill.
Ilex verticillata (L.) Gray
Potentilla fruticosa L.
Pyrus arbutifolia (L.) L. f.
Solanum dulcamara L.
Spiraea latifolia Borkh.
" *tomentosa* L.[4]

HERBS

Aster novae-angliae L.
" *paniculatus* Lam.
Epilobium molle Torr.
Eupatorium perfoliatum L.
Gentiana andrewsii Griseb.
" *crinita* Froel.
Helenium autumnale L.
Iris versicolor L.
Lobelia syphilitica L.
Lythrum salicaria L.
Ludvigia alternifolia L.
Peltandra virginica (L.) Kunth[5]
Penthorum sedoides L.[4]
Podophyllum peltatum L.
Sagittaria latifolia Willd.[4]
Scutellaria lateriflora L.
Thalictrum polygamum Muhl.
Vernonia noveboracensis Willd.

FERNS

Aspidium cristatum (L.) Sw.
Scolpendrium vulgare Sm.
Woodwardia virginica (L.) Sm.

9. Bog Association

(Equivalent of 18, 19 and 20 in fig. 2. See figs. 25, 26, and 27.)

a. Taxonomic Studies

TREES

Acer rubrum L.	Red maple
Betula populifolia Marsh.	Gray birch
* *Larix laricina* (DuRoi) Koch	American larch
* *Quercus palustris* Muench.	Pin oak
Ulmus american L.	American elm

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[4] See Mitchell, '26.

[5] See Hart, '28.

SHRUBS

Amelanchier spicata (Lam.) C. Koch	Juneberry
Andromeda glaucophylla Link	Bog rosemary
**Betula pumila* L.	Swamp birch
Chamaedaphne calyculata (L.) Moench.	Leather leaf
Gaylussacia baccata (Wang) C. Koch	Black huckleberry
Ilex verticillata (L.) Gray	Black alder
Kalmia angustifolia L.	Sheep laurel
" *polifolia* Wang.	Pale laurel
Lyonia ligustrina (L.) DC.	Male berry
Rhododendron viscosum (L.) Torr.	Clammy azalea

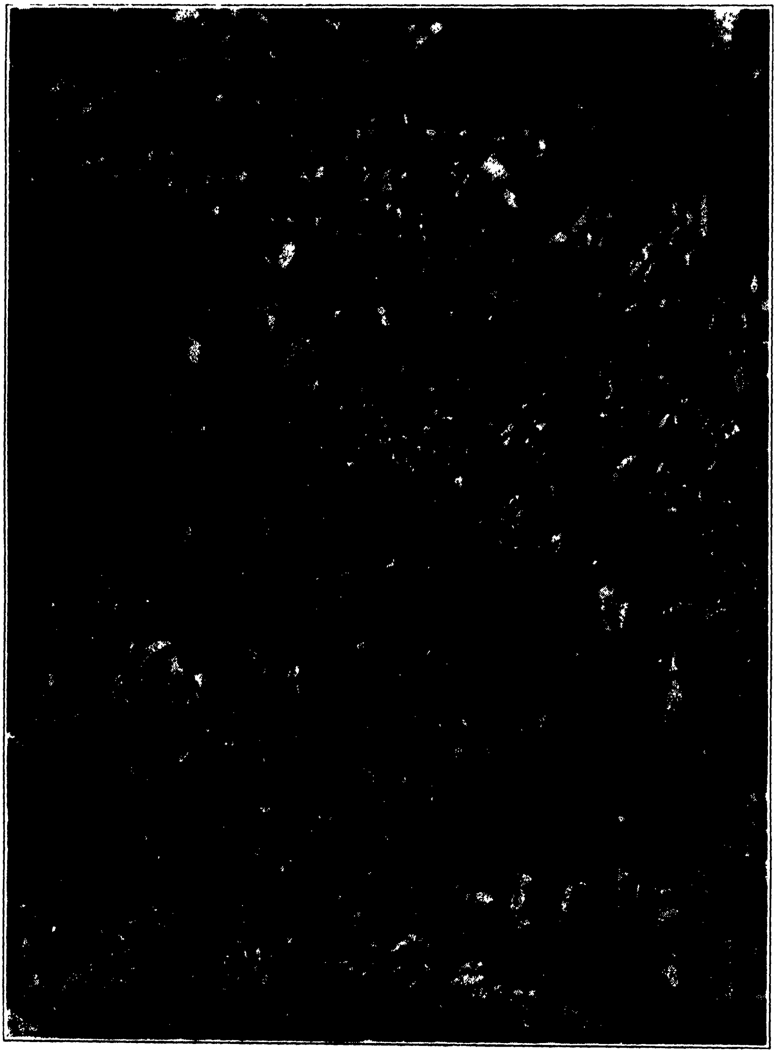

FIG. 25. The *Sarracenia purpurea* L. as seen in the bog association.

**Rubus triflorus* Richards	Dwarf raspberry
**Salix candida* Flügge	Hoary willow
" *discolor* Muhl.	Glaucous willow
Vaccinium corymbosum L.	High blueberry
" " var. *pallidum* (Ait.) Gray	" "
" *macrocarpon* Ait.	Large cranberry
" *oxycoccos* L.	Small cranberry
Viburnum dentatum L.	Arrow-wood

Fig. 26. Two months' old seedlings of *Orontium aquaticum* L. raised in the Out-of-door Laboratory.

HERBS

Arisaema triphyllum (L.) Schott.	Jack-in-the-pulpit
Cicuta bulbifera L.	Water hemlock
Cypripedium acaule Ait.	Stemless lady's slipper
Decodon verticillatus (L.) Ell.	Water willow
Drosera rotundifolia L.	Round-leaved sundew
Eriophorum callitrix Cham.	Hare's tail
" *tenellum* Nutt.	Cotton grass
Galium palustre L.	Bed straw
" *triflorum* Michx.	Sweet-scented bedstraw
Geum rivale L.	Purple avens
Lysimachia terrestris (L.) BSP.	Loosestrife
" *thrysiflora* L.	Tufted loosestrife
Maianthemum canadense Desf.	Wild lily-of-the-valley

Menyanthes trifoliata L.	Buckbean
Orontium aquaticum L.	Golden club
Pogonia ophioglossoides (L.) Ker.	Pogonia
Potentilla palustris (L.) Scop.	Marsh five-finger
Sarracenia purpurea L.	Pitcher plant
Sium cicutaefolium Schrank	Water parsnip
Thalictrum dioicum L.	Meadow rue
Typha latifolia L.	Cat-tail
Viola conspersa Reichenb.	Violet
" *pallens* (Banks) Brainerd	Sweet white violet

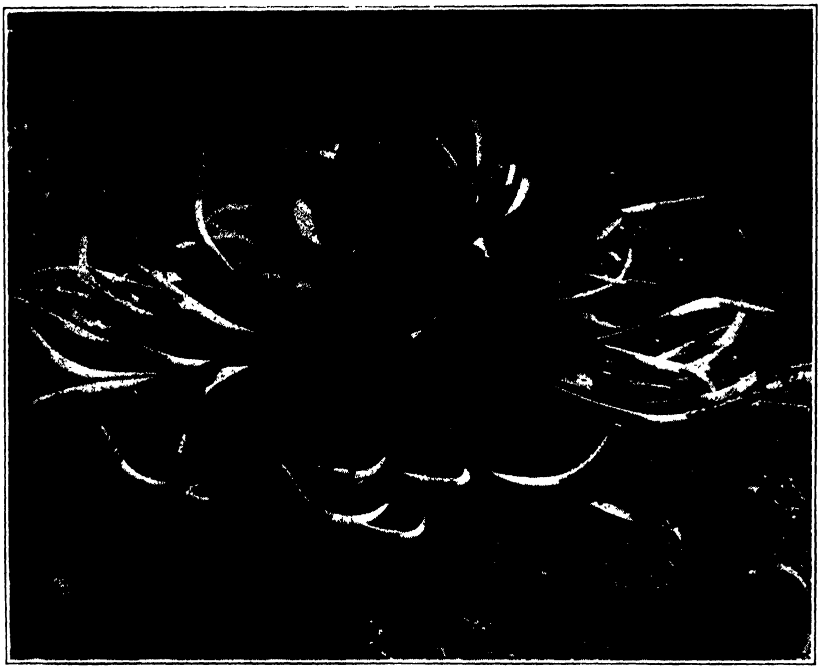

FIG. 27. A mature *Orontium aquaticum* L. plant established in the bog association.

FERNS

Aspidium cristatum (L.) Sw.	Shield fern
" *spinulosum* (O. F. Müller) Sw.	Wood fern
" *thelypteris* (L.) Sw.	" "
Equisetum palustre L.	Horsetail
Onoclea sensibilis L.	Sensitive fern
Osmunda regalis L.	Flowering fern

b. Morphological Studies

SHRUBS

Rhododendrum viscosum (L.) Torr.

Vaccinium macrocarpon Ait.

HERBS

Orontium aquaticum L.

c. Physiological Studies

SHRUBS

Kalmia angustifolia L.
Lyonia ligustrina (L.) DC.
Vaccinium macrocarpon Ait.
Viburnum dentatum L.

HERBS

Orontium aquaticum L.
Sarracenia purpurea L.

FERNS

Aspidium thelypteris (L.) Sw.
Selaginella apus (L.) Spring.

10. RAVINE ASSOCIATION

(Equivalent of 28, 29 and 30 in fig. 2. See figs. 28 and 29.)

a. Taxonomic Studies

TREES

Acer pennsylvanicum L.	Striped maple
" _saccharum_ Marsh.	Sugar maple
" _spicatum_ Lam.	Mountain maple
Betula alba L.	White birch
" _lenta_ L.	Black birch
" _lutea_ Michx. f.	Yellow birch
Carpinus caroliniana Walt.	Ironwood
Carya cordiformis (Wang.) K. Koch	Bitter nut
Cornus florida L.	Flowering dogwood
Fagus grandifolia Ehrh.	Beech
Fraxinus americana L.	White ash
Juglans cinerea L.	Butternut
Liriodendron tulipifera L.	Tulip tree
*_Salix babylonica_ L.	Weeping willow
" _nigra_ Marsh.	Black willow
Thuja occidentalis L.	Arbor vitae
Tilia americana L.	Basswood
Tsuga canadensis (L.) Carr.	Hemlock

SHRUBS

Alnus incana (L.) Moench.	Hoary alder
" _rugosa_ (DuRoi) Spreng.	Smooth alder
Amelanchier canadensis (L.) Medic.	Shad bush
Hamamelis virginiana L.	Witch-hazel
Kalmia latifolia L.	Mountain laurel
Lonicera canadensis Marsh.	American fly honeysuckle
*_Rhododendron maximum_ L.	Great laurel
Salix cordata Muhl.	Willow
" _discolor_ Muhl.	Glaucous willow
* " _glaucophylla_ Bebb.	Willow
" _lucida_ Muhl.	Shining willow
Taxus canadensis Marsh.	American yew
*_Viburnum alnifolium_ Marsh.	Hobble-bush

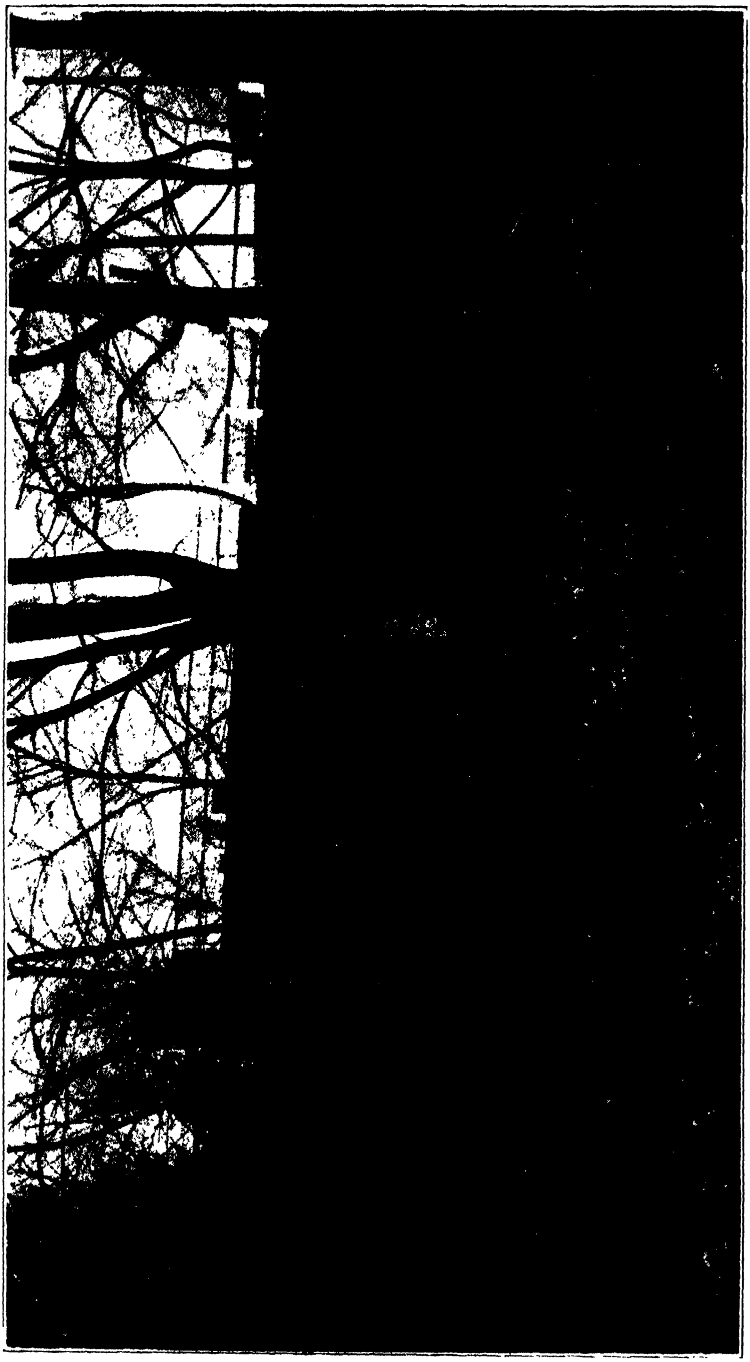

FIG. 28. An early stage in the development of the hemlock ravine association.

FIG. 29. A hemlock ravine in the County in 1931, with maidenhair fern.

HERBS

*_Actaea alba_ (L.) Mill.	White baneberry
* " _rubra_ (Ait.) Willd.	Red baneberry
Aquilegia canadensis L.	Wild columbine
Arabis lyrata L.	Rock cress
Aralia racemosa L.	Spikenard
Arisaema dracontium (L.) Schott.	Green dragon
" _triphyllum_ (L.) Schoff.	Jack-in-the-pulpit
Asarum canadense L.	Wild ginger
Asclepias incarnata L.	Swamp milkweed
Campanula rotundifolia L.	Bluebell
Chrysoplenium americanaum Schwein.	Golden saxifrage
*_Cornus canadensis_ L.	Bunchberry
Corydalis sempervirens L.	Pale corydalis
*_Cypripedium acaule_ Ait.	Stemless lady's slipper
Dicentra cucullaria (L.) Bernh.	Dutchman's breeches
Epifagus virginiana (L.) Bart.	Beech-drops
Erythronium americanum Ker.	Yellow adder's tongue
Eupatorium perfoliatum L.	Boneset
Eupatorium purpureum L.	Joe-Pye weed
Heuchera americana L.	Common alum root
Maianthemum canadense Desf.	Maianthemum
Medeola virginiana L.	Indian cucumber-root
Mitchella repens L.	Partridge berry
Mitella diphylla L.	Bishop's cap
Oxalis acetosella L.	Common wood sorrel
" _violacea_ L.	Violet wood sorrel
Parnassia caroliniana Michx.	Grass of Parnassus
Pilea pumila (L.) Gray	Clearweed
Polygonatum biflorum (Walt.) Ell.	Small Solomon's seal
Potentilla argentea L.	Silvery cinquefoil
" _tridentata_ Ait.	Three-toothed cinquefoil
Prenathes alba L.	White lettuce
Sagina nodosa (L.) Fenzl.	Pearlwort
*_Sanguisorba minor_ Scop.	Garden burnet
Saxifraga virginiensis Michx.	Early saxifrage
Sedum acre L.	Mossy stonecrop
Smilacina racemosa (L.) Desf.	False spikenard
Streptopus roseus Michx.	Twisted-stalk
Thalictrum dioicum L.	Early meadow rue
" _revolutum_ DC.	Meadow rue
Trientalis americana (Pers.) Pursh.	Star flower
Trillium declinatum (Gray) Gleason	Wake robin
" _erectum_ L.	" "
* " _grandiflorum_ (Michx.) Salisb.	" "
* " _undulatum_ Willd.	Painted trillium
Uvularia grandiflora Sm.	Bellwort
" _perfoliata_ L.	"
Viola blanda Willd.	Violet
" _palmata_ L.	"
" _rostrata_ Pursh.	Long-spurred violet
" _rotundifolia_ Michx.	Early yellow violet

FERNS

Adiantum pedatum L.	Maidenhair
Aspidium marginale (L.) Sw.	Shield fern
" " var. *elegans* J. Robinson	" "
" *noveboracense* (L.) Sw.	Wood fern
" *spinulosum* (O. F. Müller) Sw.	" "
Asplenium acrostichoides Sw.	Spleenwort
" *platyneuron* (L.) Oakes	"
* " *ruta-muraria* L.	"
" *trichomanes* L.	"
**Botrychium virginianum* (L.) Sw.	Rattlesnake fern
Camptosorus rhizophyllus (L.) Link.	Walking leaf fern
**Cryptogramma stelleri* (Gmel.) Prantl.	Rock brake
Cystopteris bulbifera (L.) Bernh.	Bladder fern
" *fragilis* (L.) Bernh.	" "
Equisetum pratense Ehrh.	Horsetail
Onoclea sensibilis L.	Sensitive fern
**Pellaea atropurpurea* (L.) Link.	Cliff brake
Phegopteris dryopteris (L.) Fée	Oak fern
" *hexagonoptera* (Mx.) Fée	Beech fern
" *polypodioides* Fée	Oak fern
Polypodium vulgare L.	Polypody
Polystichum acrostichoides (Michx.) Schott.	Christmas fern
" " var. *schweinitzii* (Beck) Small.	" "
Selaginella rupestris (L.) Spring.	Selaginella
Woodsia ilvensis (L.) R. Br.	Woodsia
" *obtusa* (Spreng.) Torr.	"

b. Morphological Studies

HERBS

Aralia racemosa L.

Arisaema triphyllum (L.) Schott.

c. Physiological Studies

TREES

Acer spicatum Lam.
Carpinus caroliniana Walt.
Betula lenta L.

SHRUBS

Amelanchier canadensis (L.) Medic.

HERBS

Actea alba (L.) Mill.
Aralia racemosa L.
Arisaema triphyllum (L.) Schott.
Campanula rotundifolia L.
Dicentra cucullaria (L.) Bernh.

11. Stream-side Association

(Equivalent of 22, 23, 24, 25 and 26 in fig. 2. See figs. 30 and 31.)

a. Taxonomic Studies

TREES

**Acer negundo* L.	Box elder
" *rubrum* L.	Red maple
" *saccharinum* L.	Silver maple
Carpinus carolinianum Walt.	Ironwood
Carya cordiformis (Wang.) K. Koch	Bitternut
" *glabra* (Mill.) Spach.	Pignut
* " *ovata* (Mill.) K. Koch	Shag-bark hickory

Fig. 30. The stream-side association in the making. A path under construction.

**Celtis occidentalis* L.	Hackberry
Crataegus crus-galli L.	Hawthorn
* " *fecunda* Sarg.	"
Fraxinus americana L.	White ash
* " *nigra* Marsh.	Black ash
* " *pennsylvanica* Marsh.	Red ash
**Juglans cinerea* L.	Butternut
" *nigra* L.	Black walnut
**Liquidambar styraciflua* L.	Sweet gum
**Morus rubra* L.	Red mulberry
Ostrya virginiana (Mill.) K. Koch	Hop hornbeam
Platanus occidentalis L.	Sycamore
Populus balsamifera L.	Balsam poplar
Prunus nigra Ait.	Canada plum
**Quercus bicolor* Willd.	Swamp white oak
* " *macrocarpa* Michx.	Bur oak
* " *palustris* Muench.	Pin oak

**Salix babylonica* L.	Weeping willow
" *lucida* Muhl.	Shining willow
" *nigra* Marsh.	Black willow
Tilia americana L.	Basswood
Ulmus americana L.	American elm
" *fulva* Michx.	Slippery elm

FIG. 31. The stream-side association in the Out-of-door Laboratory as it appeared in 1931, from the same point as fig. 30.

SHRUBS

Alnus incana (L.) Moench.	Hoary alder
* " *rugosa* (Do Roi) Spreng.	Smooth alder
Amelanchier canadensis (L.) Medic.	Shad bush
Amorpha fruticosa L.	False indigo
Benzoin aestivale (L.) Nees.	Spice bush
Clematis virginiana L.	Virgin's bower
**Clethra alnifolia* L.	Sweet pepper bush
**Cornus amomum* Mill.	Kinnikinnik
" *stolonifera* Michx.	Red-osier dogwood
Hamamelis virginiana L.	Witch-hazel
Ilex verticillata (L.) Gray	Black alder
Menispermum canadense L.	Moonseed
**Myrica gale* L.	Sweet gale
**Physocarpus opulifolius* (L.) Maxim.	Nine-bark

Psedera quinquefolia (L.) Greene	Woodbine
Rosa carolina L.	Rose
" *virginiana* Mill.	"
Salix cordata Muhl.	Willow
" *discolor* Muhl.	"
Sambucus canadensis L.	Elder
Solanum dulcamara L.	Bittersweet
Spiraea latifolia Borkh.	Meadow-sweet
Spiraea tomentosa L.	Steeple bush
Staphylea trifolia L.	Bladdernut
Viburnum acerifolium L.	Arrow-wood
" *dentatum* L.	"
" *lentago* L.	Nannyberry
Vitis cordifolia Michx.	Frost grape
" *vulpina* L.	River bank grape

HERBS

Acorus calamus L.	Sweet flag
Alisma plantago-aquatica L.	Water plantain
Anemone quinquefolia L.	Wood anemone
Angelica atropurpurea L.	Angelica
Arisaema dracontium (L.) Schott.	Green dragon
" *triphyllum* (L.) Schott.	Jack-in-the-pulpit
Asarum canadense L.	Wild ginger
Asclepias incarnata L.	Swamp milkweed
Aster lateriflorus (L.) Britt.	Aster
" *paniculatus* Lam.	"
" *puniceus* L.	"
" *vimineus* Lam.	"
Caltha palustris L.	Marsh marigold
Campanula aparinoides Pursh.	" bluebell
Cassia marilandica L.	Wild senna
Chelone glabra L.	Turtlehead
Chrysosplenium americanum Schwein.	Golden saxifrage
Claytonia virginica L.	Spring beauty
Clematis virginiana L.	Virgin's bower
Convolvulus sepium L.	Hedge bindweed
Dentaria diphylla Michx.	Toothwort
" *laciniata* Muhl.	"
Dicentra cucullaria (L.) Bernh.	Dutchman's breeches
Dioscorea villosa L.	Wild yam-root
Echinocystis lobata (Michx.) T. & G.	" balsam-apple
Erythronium americanum Ker.	Yellow adder's tongue
Eupatorium perfoliatum L.	Boneset
" *purpureum* L.	Joe Pye weed
Gentiana andrewsii Griseb.	Closed gentian
" *crinita* Froel.	Fringed gentian
Geranium maculatum L.	Cranesbill
Habenaria lacera (Michx.) R. Br.	Ragged fringed orchis
" *psychodes* (L.) Sw.	Fringed orchis
Helenium autumnale L.	Sneezeweed
Heracleum lanatum Michx.	Cow parsnip
Hibiscus moscheutos L.	Swamp rose mallow

Houstonia caerulea L.	Bluets
Humulus lupulus L.	Common hop
Hypericum ascyron L.	Great St. John's-wort
“ _canadense_ L.	St. John's-wort
Impatiens biflora Watt.	Spotted touch-me-not
“ _pallida_ Nut.	Pale touch-me-not
*_Iris pristimatica_ Pursh.	Slender blue flag
“ _versicolor_ L.	Larger blue flag
Lilium canadense L.	Wild yellow lily
“ _philadelphicum_ L.	Wood lily
Lobelia cardinalis L.	Cardinal flower
“ _siphilitica_ L.	Great lobelia
Lysimachia nummularia L.	Moneywort
Mentha piperita L.	Peppermint
“ _spicata_ L.	Spearmint
*_Mertensia virginica_ (L.) Link.	Virginia cowslip
Mikania scandens (L.) Willd.	Climbing hemp-weed
Myosotis laxa Lehm.	Forget-me-not
“ _scorpioides_ L.	True forget-me-not
Oakesia sessilifolia (L.) Wats.	Oakesia
*_Orobanche uniflora_ L.	One-flowered cancer-root
Peltandra virginica (L.) Kunth.	Arrow arum
Petasites palmatus (Ait.) Gray	Sweet coltsfoot
Podophyllum peltatum L.	May apple
Polygonatum biflorum (Walt.) Ell.	Small Solomon's seal
“ _commutatum_ (R. & S.) Dietr.	Great Solomon's seal
Polygonum convolvulus L.	Black bindweed
“ _scandens_ L.	Climbing false buckwheat
Pontederia cordata L.	Pickerel-weed
Ranunculus abortivus L.	Small-flowered crowfoot
“ _septentrionalis_ Poir.	Swamp buttercup
Rudbeckia laciniata L.	Cone-flower
Sagittaria latifolia Willd.	Arrow-head
Sanguinaria canadensis L.	Bloodroot
Scutellaria galericulata L.	Skullcap
“ _lateriflora_ L.	Mad-dog skullcap
*_Sicyos angulatus_ L.	One-seeded bur cucumber
Sisyrinchium angustifolium Mill.	Blue-eyed grass
* “ _gramineum_ Curtis	“ “
Sium cicutaefolium Schrank.	Water parsnip
Smilacena racemosa (L.) Desf.	False spikenard
“ _stellata_ (L.) Desf.	“ Solomon's seal
Smilax herbacea L.	Green brier
“ _rotundifolia_ L.	“ “
Solidago elliottii T. & G.	Golden-rod
Spiranthes romanzoffiana Cham.	Ladies tresses
Steironema ciliatum (L.) Raf.	Yellow June lily
Symphytum officinale L.	Common comfrey
Thalictrum dioicum L.	Early meadow rue
“ _polygamum_ Muhl.	Tall meadow rue
Thaspium aureum Nutt.	Meadow parsnip
Trillium cernuum L.	Wake robin
“ _erectum_ L.	“ “
* “ _grandiflorum_ (Michx.) Salisb.	“ “

Uvularia grandiflora Sm.	Bellwort
" *perfoliata* L.	"
Veratum viride Ait.	False hellebore
Verbena hastata L.	Blue vervain
Veronica americana Schwein.	American brooklime
" *anagallis-aquatica* L.	Water speedwell
" *virginica* L.	Culver's root
Viola blanda Willd.	Violet
" *cucullata* Ait.	"
" *pallens* (Banks) Brainerd	Sweet violet
" *scabriuscula* Schwein.	Smooth yellow violet
" *sororia* Willd.	Violet

FERNS

Aspidium cristatum (L.) Sw.	Shield fern
" *noveboracense* (L.) Sw.	Wood fern
" *spinulosum* (O. F. Müller) Sw.	" "
" *thelypteris* (L.) Sw.	" "
Cystopteris fragilis (L.) Bernh.	Bladder fern
Onoclea sensibilis L.	Sensitive fern
" *struthiopteris* (L.) Hoffm.	Ostrich fern
Osmunda cinnamomea L.	Cinnamon fern
" *claytoniana* L.	Flowering fern
" *regalis* L.	" "
Woodwardia virginica (L.) Sm.	Chain fern

b. Morphological Studies

SHRUBS

Benzoin aestivale (L.) Nees
Ilex verticilata (L.) Gray

HERBS

Alisma plantago-aquatica L.
Caltha palustris L.
Iris versicolor L.
Cassia marilandica L.
Chelone glabra L.
Polygonatum commutatum (R. & S.) Dietr.

c. Physiological Studies

TREES

Celtis occidentalis L.
Acer negundo L.
Acer rubrum L.

HERBS

Alisma plantago-aquatica L.
Asclepias incarnata L.
" *syriaca* L.
Aster puniceus L.
Caltha palustris L.
Cassia marilandica L.
Chelone glabra L.
Dioscorea villosa L.[4]
Eupatorium purpureum L.[4]
Gentiana crinita Froel.
Hesperis matronalis L.[4]
Hibiscus moscheutos L.
Lobelia cardinalis L.[4]
Mimulus ringens L.[4]
Polygonatum commutatum (R. & S.) Dietr.
Smilax herbacea L.
Steironema ciliatum (L.) Raf.
Verbena hastata L.[4]
Veronica virginica L.

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[4] See Mitchell, '26.

FERNS

Onoclea struthiopteris (L.) Hoffm.	*Osmunda claytoniana* L.
Osmunda cinnamomea L.	" *regalis* L.

CONCLUSION

1. This development of an Out-of-door Laboratory for Experimental Ecology in conjunction with other studies has been of assistance in the presentation of ecology. The very establishment of the plants in the laboratory has supplied valuable data.

2. Twenty-eight of the thirty associations of the county are so well established that fifty per cent of their plant members are at hand for taxonomic, morphological and physiological studies.

3. This type of laboratory will never be finished. Its very dynamic character makes this impossible. The development of the Dutchess County Botanical Garden as an Out-of-door Laboratory for Experimental Ecology offers the department opportunities for class and research work for an indefinite period. There are unlimited possibilities for research problems, of such a nature, that they may be started in the laboratories and completed here or elsewhere as graduate studies.

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REVIEWS

RECORDS OF ENVIRONMENTS[1]

Sedimentary rocks compose the substratum of many environments; sediments, during transport and deposition, form important factors in survival. They, and the fossils in them, constitute direct records of past environments and of organic responses thereto. It is essential, therefore, that sedimentary processes and results enter into any historical consideration of organic aggregations, or of the distribution of ancient groups.

Until within the last two decades, such consideration has been hampered by the scanty attention which geologists themselves had given to sedimentary rocks and the factors involved in their deposition. During that time, however, so much has been done that the results are confusing. The " Treatise on Sedimentation " is an attempt to organize them in one compact volume at once suited to the student, the specialist, and the inquirer who requires reliable summaries supported by adequate references.

In the main, this attempt has been successful. Though most of it has been written by Dr. Twenhofel, the book was prepared by a large number of specialists and so has the value of a symposium. It covers the entire field of sedimentology, summarizing the work of some 1200 authors, to whose papers it gives 2250 references. Most of the summaries are as modern as can be consistent with adequate synthesis, and references to papers of 1930 and 1931 are surprisingly frequent. An elaborate table of contents and an index of 24 pages aid the search for specific information.

Four chapters have special significance to the biologist. One of these (Chapter III) relates the specific environment and its records to general topographic and climatic conditions—relationship of special significance in dealing with the backgrounds of marine sedimentation. Chapter IV discusses the influence of organisms upon deposits and conditions of deposition, with special emphasis on animals. Here Dr. Twenhofel relies somewhat too much on the present as a guide to the past—the reason probably being that little has been done with the ecology of fossil invertebrates. Those best known are discussed adequately, and critically, in the section on organic limestones. Chapter VI, on " Structures, Textures and Colors of Sediments," presents the most reliable data available for the recognition of physical factors in past environments, again based on those of the present. It shows the need for close correlation between ecologic, paleontologic and geologic studies if the history of environmental types is to be determined.

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[1] **Twenhofel, William,** and Collaborators. 1932. Treatise on Sedimentation. Second Edition, Completely Revised. Pages xxix + 926, 121 figs. *Williams and Wilkins, Baltimore.* $8.00.

Such correlation is attempted in Chapter VI. Dealing with environments of sedimentation, it summarizes the inorganic side of paleoecology. Without offering guidance to the ecologist, it provides material of substantial value to biogeography, which is more intimately linked with the past than sometimes is realized. Probably it performs an even greater service by showing paleontologists how they may think in terms of active processes, and so bring their faunal studies in line with established trends of biology proper.

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MEDICAL ENTOMOLOGY[1]

This is a revision of the first textbook of medical entomology published in the United States ("Handbook of Medical Entomology" published in 1915 by the same authors). The revised volume follows the high standard of excellence set by the earlier book and also brings the review of our information in this field up to date. It has been entirely rewritten and much enlarged. The chief difference in the two editions is one of arrangement; the latter one being arranged according to the systematic order of the forms considered, rather than according to etiological agents of the diseases transmitted, as in the earlier edition.

After three introductory chapters, there follow three chapters on the Arachnida (including the Spiders, Scorpions, Mites, and Ticks), and one on the Centipedes and Millipedes, then a chapter on the structure and development of insects, and one on the systematics of the true insects. Then, in order, come chapters on the Lice, Bugs (Hemiptera), Beetles, Moths and Butterflies, and an introductory chapter on flies in which some of the smaller Diptera and the diseases transmitted by them are considered. Eight further chapters are devoted to the various kinds of Diptera, as follows: Culicidae or Mosquitoes; Mosquitoes and disease; Measures for avoidance and extermination of Mosquitoes; Other blood-sucking diptera; Botflies; House flies and their allies; Glossina, or Tsetse flies; and Myiasis. There is a chapter on the fleas and one upon Hymenoptera. An appendix contains instructions for fumigation against household insects. An extensive bibliography covers most of the more important original articles.

The authors seem to have given just the right proportion of emphasis upon structure, taxonomy, biology, relationship to disease, and control of the various forms to make the book interestingly readable. The book should prove to be very valuable as a textbook for courses in medical entomology and, also,

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[1] **Riley, W. A., and O. A. Johannsen.** 1932. Medical Entomology. A survey of insects and allied forms which affect the health of man and animals. Pages xi + 476, 184 figs. *McGraw-Hill Book Co., Inc., New York.* $4.50.

as a reference book for students interested in the ecological adjustments of the parasites of man and domestic animals.

Clay G. Huff

University of Chicago

The Technique of Plant Distribution

There have been many accounts of the means by which various plants are distributed but the present author[1] approaches the subject from a somewhat different angle. His contribution consists of a detailed classification of the methods of ecological distribution of plants, amounting to an extensive annotated bibliography combined with an encyclopedic glossary of the technical terminology of the subject. The list of the most important disseminative technical terms includes over one hundred.

Methods of ecological distribution include several types, allochory, or distribution by foreign agents, subdivided into anemochory, distribution by wind; hydrochory, distribution by water; zoochory, distribution by animals; and anthropochory, distribution by man. Each of these categories is again subdivided.

Anemochory includes anemogravichory, distribution by horizontal air currents *above* the surface of the earth; anemogeochory, distribution by horizontal air currents *along* the surface of the earth; anemochionochory, distribution by horizontal air currents over the surfaces of snow and ice fields; anemoheliochory, distribution by vertical air currents and later by horizontal currents at higher levels; and anemoturbochory, distribution by storms (as tornadoes).

Hydrochory has two subdivisions: limnochory, distribution by fresh water; and thalassochory, distribution by sea water.

Zoochory and anthropochory have parallel subdivisions: epizoochory and epianthropochory, transport of disseminules (or burs and other adherent fruits, etc.) upon the body; endozoochory and endoanthropochory, transport within the body by means of ingestion and later ejection of disseminules; and synzoochory and synanthropochory, intentional collecting and storing of seeds and fruits as in nests of ants, rodents and birds, or by man.

There are also several forms of autochory or self-distribution, such as blastochory, distribution from the mother plant by outgrowths such as runners, rhizomes, etc.; bolochory, propulsion from the mother plant as by exploding fruits, or euautochory, distribution by self-propelled disseminules such as swarm spores or hygroscopic fruits and seeds.

If only one agent is involved in the transport, the method is haplochory; but when two agents are concerned it is designated as some form of diplochory or if both are animals, as diplozoochory.

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[1] **Heintze, Aug.** Handbuch der Verbreitungsökologie der Pflanzen. Lief. 1., pp. 1–134. Published by the author: Stockholm. 1932.

Time and distance as well as motive agents are recognized as factors in ecological distribution. Tachychory refers to distribution of disseminules immediately after ripening, while bradychory refers to delayed distribution. Transport to places within one kilometer of the nearest mother plant is called "nahverbreitung" or near-distribution; carriage from one to ten kilometers is "langverbreitung" or long-distribution, while removal to places more than ten kilometers from the nearest mother plant is "fernverbreitung" or distance distribution.

The disseminules themselves are classified into fructifications and vegetative reproductive organs. Fruiting bodies are divided into three main groups: (1) above ground fruits, including nuts, dry seeds and fruits (adherent fruits, saccate fruits, needlelike fruits, winged fruits, glandular fruits, swimming fruits, fruits with flight hairs), soft or fleshy fruits as berries, arils and fleshy cones; (2) subterranean fruits such as those of amphicarpous or geocarpous plants; and (3) fruiting fragments or entire fruiting plants which migrate, such as *Potomogeton, Callitriche,* etc.

The vegetative disseminules are likewise divided into three groups: (1) migrating shoots and roots which distribute the species by growth; (2) "wanderknospen" such as bulbs, tubers, etc., and (3) "wander-fragmente" including detached vegetative reproductive structures.

Part two is an historical survey of the subject in which the origin and development of the terminology is traced. Most of it has evolved since Linnaeus, but Sloane (1696) and Rumphius (1702) are mentioned as contributors. Linnaeus started the ball rolling and it has been kept going to Holmberger, Sprengle, Lidbeck, Lyell, Alph. De Candolle, Kerner, Schimper, Sernander, Guppy, Heintze and others. An extensive bibliography is presented.

Part three advises the student seeking an introduction to methods of research in the ecological distribution of plants to make a study of tychoepiphytes since these are generally common in most regions and their agents of distribution are few and well known. Moreover the facts can be easily checked by first hand observations. The trees and shrubs bearing these facultative epiphytes were originally designated as host-plants; but Barnewitz and others have suggested a better term (tragenpflanzen), supporting plants. Records of the phenomenon of tychoepiphytism date as far back as Theophrastus (371–286 B. C.), and Pliny the Elder (79 B. C.). The first detailed account, however, was that of Preuschoff (1882), who found 47 species of phanerogams and ferns on pollarded willows in West Prussia. His paper, however, appeared in a little yearbook and was unnoticed for a long time. The author (Heintze) reports in some detail his own results of many years of careful and extensive studies of tychoepiphytism in the crowns and on the stems of pollarded willows at Skane, Sweden. He also reports investigations of tychoepiphytes in southern Sweden, in the Tyrol, Austria, and in Trentino, Italy. In each case the examples are grouped according to the method of their transport to the supporting tree. The number of specimens, their fertility, location, mode and time of distribution, minimum distance from the nearest mother plant, are listed for each of the numerous species of tychoepiphytes mentioned. Synanthropochory, endozoochory, epizoochory, synzoochory, diplozoochory, anemochory and blastochory were all found responsible for transport of tychoepiphytes to their respective tragenpflanzen. At Skane, Sweden, alone 32 species of shrubs and trees, and over 100 herbaceous forms were founded in the crowns of pollarded willows, while on the stems of these there occurred four woody species and 54 herbs. On the crowns of other trees, including oak, ash, linden, elm, and *Acer negundo,* were found 29 tychoepiphytic trees and shrubs, and 55 herbs. At Tyrol 19 woody and 41 herbaceous species were listed, and in north Italy 28 woody and 45 herbabaceous tychoepiphytes were found.

HELEN DIXON

THE UNIVERSITY OF CHICAGO

ECOLOGICAL LITERATURE RECEIVED

Jalava, Matti. 1932. Puun kosteuspitoisuuden, koon ja muodon muutoksista (Changes in the moisture content, volume and form of wood). Summary in English. *Metsätieteellisen Tutkimuslaitoksen Julkaisuja 18.2 Communicationes Instituti Forestalis Fenniae 18.2.*

Old, M. C. 1932. Environmental Selection of the Fresh-water Sponges (Spongillidae) of Michigan. *Trans. Am. Micr. Soc.,* 51: 129–136.

Whiting, P. W. 1932. Reproductive Reactions of Sex Mosaics of a Parasitic Wasp, *Habrobracon juglandis. Journ. Comp. Psychology,* 14: 345–363.

Wheeler, W. M. 1932. An Extraordinary Ant-guest from the Philippines. *Livre du Centenaire. Soc. Ent. France.*

Alverdes, F. 1932. The Psychology of Animals. *Harcourt, Brace and Co., New York.*

Ashton, Ruth E. 1932. Plants of Rocky Mountain National Park. iv + 157 *pp.* 100 *figs.* 15 *pl. National Park Service, Washington, D. C.*

Over, Wm. H. 1932. Flora of South Dakota. 161 *pp.* 32 *figs. Univ. So. Dakota, Vermillion, S. D.* $1.00.

Salisbury, E. J. 1932. The East Anglian Flora. *Trans. Norfolk and Norwich Nat. Soc.,* 13: 191–263. 8 *pl.* 106 *maps.*

Erdtman, G. 1932. Literature on pollen statistics and relative topics published 1930 and 1931. *Geogl. Fören. Förh. Stockholm,* 54: 395–418. 3 *figs.*

PROCEEDINGS

BUSINESS MEETINGS OF THE ECOLOGICAL SOCIETY OF AMERICA AT ATLANTIC CITY, N. J., DECEMBER 28, AND DECEMBER 29, 1932

MEETING OF DECEMBER 28, 1932

The Society met at 11:45 A.M. with President Nichols presiding.

The Secretary reported a successful meeting of the Society at Syracuse, N. Y., June 21–23 in conjunction with the Botanical Society of America and Section F, A. A. A. S.

The Secretary reported the following appointments made by the President during the year.

Dr. G. D. Fuller to represent the Society on the Council of the Union of American Biological Societies to succeed A. O. Weese.

Dr. A. O. Weese as chairman of a subcommittee of the Committee on the Preservation of Natural Conditions to provide for the acquisition of lands by Universities for instruction and research.

Drs. V. E. Shelford, chairman, W. C. Allee, and E. B. Powers a committee to arrange a symposium at the Chicago meeting centering around August Krogh, the Danish Zoologist.

Dr. W. E. Allen's appointment confirmed as representative of the Society at the Fifth Pacific Science Congress.

Dr. Charles Kraebel, the western representative of the Society on the Pacific Division of the A. A. A. S.

A Canadian Committee on the Preservation of Natural Conditions as announced in the March Bulletin.

Other committees were appointed whose reports are included here.

The Secretary expects to publish a list of the new members in each June Bulletin such as was published in the June, 1932, Bulletin.

Report of the Committee for the Study of Plant and Animal Communities and of the Committee on the Preservation of Natural Conditions

1. Study Committee

Following the Business meeting at New Orleans at which the committee reported a plan for nature sanctuaries which was adopted by the Society, a conference on nature sanctuaries was held at Tulane University, December 30, 1931, which was attended by representatives of the Ecological Society, the United States Forest Service, The Izaak Walton League, the National Park

Service, the United States Biological Survey, the American Ornithological Union, the Wilson Ornithological Club, the National Parks Association, the Game Survey (Sporting Arms and Ammunition Manufacturers Institute), and the National Research Council. The participants agreed to the principle of nature sanctuaries surrounded by buffer areas and further agreed that these areas should be left alone without management and that only in the case of an emergency that might arise should control measures be undertaken and then only after most careful consideration and determination as to their practical necessity. The full text of the report and personnel may be found in *Science,* 75: 481, May 6, 1932 (the names of the Wilson Ornithological Club and its representative, Dr. Lynds Jones, were accidentally omitted from this account).

Many suggestions were brought to the attention of the committee at this conference and were embodied in a statement or memorandum on nature sanctuaries which was circulated to the Advisory Board twice, revised and enlarged and then submitted again to the Board. The suggestions of Dr. J. Grinnell, the late Dr. H. M. Hall, and Dr. H. C. Bryant were especially extensive and valuable. This final draft constitutes the most important part in the Committee's report. The complete text of the memorandum and long explanatory introduction is available in mimeographed form to members of the Society who apply for it and to other interested persons. The complete text with a somewhat abbreviated introduction will be found in this issue of ECOLOGY. The committee recommended discussion of the nature sanctuary plan with state and federal forest and park officials as a part of the work for 1933.

A number of members of the study committee have been engaged in research on grasslands and we found that excellent work had been done on insects over a period of years in Saskatchewan, excellent work on grass roots in Nebraska and the study of mammalian effects at the University of Arizona. There were less extensive and intensive studies in North Dakota, Oklahoma and Texas. The grassland investigators authorized the chairman to apply to the National Research Council for the formation of a committee of the Council which would pass upon requests for grants to aid in completing the work in each center so that it might cover plants, invertebrates and vertebrates, especially birds and mammals. At its last meeting the Council authorized the formation of such a committee with V. E. Shelford, Chairman, and four additional members to be selected by the chairman in conference with the vice-chairman of the Division of Biology and Agriculture. Some progress has been made toward the selection of the other four members and a meeting is anticipated in the spring of 1933.

The Committee for the Study of Plant and Animal Communities also suggested that there should be a chairman of a separate sub-committee under the Committee on the Preservation of Natural Conditions to urge universities to secure examples of natural communities for research and instruction in ecological lines. Dr. A. O. Weese has accepted this chairmanship and the preliminary plans which were worked out are being turned over to him.

2. Preservation Committee

This committee is necessary because of the large number of men in government service who are on the study committee and are forbidden by law to participate in lobbying. This committee has been in correspondence with the National Parks Service regarding a crest road in the Great Smoky Mountains National Park and the committee asked the Society to pass the following resolution:

Whereas, it is the object of the Ecological Society of America to secure the reservation of certain areas in which the natural conditions in plant and animal communities may be studied and the fluctuation in abundance of the organisms ascertained,

Be it resolved that the Ecological Society of America commend the policy of the National Park Service to maintain adequate wilderness areas within the Great Smoky Mountains National Park. It approves the proposed road from Newfound Gap westwardly along the crest from gap to gap and also the program to keep the crest of the ridge eastward from Newfound Gap free from road development.

It seemed a step in the right direction to subdivide the park into a region of development and a region for a nature sanctuary.

The sub-committee on the Superior National Forest under the chairmanship of Dr. Cooper, reported through Dr. Cahn that considerable progress had been made in stopping the illegal fur-trapping which has removed very large numbers of animals. The beaver in particular has been destroyed in such large numbers that their dams have gone out of the streams and have lowered the water level so as to make canoeing, formerly quite popular in the Superior National Forest, quite impossible in many of the streams.

At the request of a Canadian member of the general committee, a committee on the Preservation of Natural Conditions in Canada was appointed. The personnel was published in the Society bulletin. The terms of the committee on the *Preservation* of *Natural Conditions* expired at the meeting. The chairman recommended that V. E. Shelford continue as chairman and be authorized to select three other members. Dr. A. R. Cahn was proposed as secretary.

The chairman recommended that the reports of the two committees be adopted including the Smoky Mountain resolution. They were unanimously adopted.

The chairman further recommended that the committees be granted $200.00 from the dues fund of the Society in so far as the treasury would permit and all royalties for the Naturalist Guide and contributions from contributing societies and individuals. The recommendation was adopted.

V. E. Shelford, *Chairman*

REPORT OF COMMITTEE ON NOMENCLATURE

The following report was read by the Secretary.

The following members were appointed by Dr. G. E. Nichols, President of the Society: Royal N. Chapman, Dean of Graduate School of Tropical Agriculture, University of Hawaii, Honolulu, Hawaii; C. F. Korstian, Professor of Forestry, Duke University, Duke Station, Durham, North Carolina; A. S. Pearse, Professor of Zoology, Duke University, Duke Station, Durham, North Carolina; Paul S. Welch, Professor of Zoology, University of Michigan, Ann Arbor, Michigan; and Herbert C. Hanson, Chairman, Professor of Botany, North Dakota Agricultural College, Fargo, North Dakota.

The Committee is formulating a working program. There is general agreement that it should serve as a clearing house to aid in avoiding confusion and duplication in the use of terms. Only a modest program will be attempted at the present time. The Committee welcomes questions regarding terms that appear to need clarification. Members are urged to submit terms for study and recommendation by the Committee. In accordance with the originally authorized duties (see ECOLOGY, 12: 437–438, 1931) the Committee cannot attempt to be dogmatic about definitions.

The work of a Committee on Nomenclature proceeds slowly, especially when the members are widely scattered. Therefore, it is recommended that this committee be continued indefinitely and that the present membership remain as at present for the next year.

HERBERT C. HANSON, *Chairman*

The report was accepted and the committee continued.

EDITORS' REPORT ON ECOLOGY

We have solicited editorial comment from at least two members of the board in addition to the editor or associate editor and we have often sent papers to other individuals especially qualified to offer constructive comment.

We have endeavored to keep the journal within the size limits suggested by our Business Manager. This has resulted in the publication of fewer pages, 424, compared to 761 for 1931.

We have tried to keep papers condensed as far as it is practicable, especially with regard to illustrations and tables. We propose to carry this policy a bit further this coming year and in general limit the number of pages to 15 and the amount of tabular and illustrative material to 20 per cent of the paper.

We propose to limit the authors to members of the Ecological Society except in special instances where non-members have distinct contributions of definite value to ecologists.

We have arranged to collect the abstracts from the authors, edit these and send them directly to Biological Abstracts from the editorial office. This should result in a more efficient abstracting service for our authors and will save the editorial office of Biological Abstracts unnecessary trouble and expense.

ALFRED EMERSON, *Editor*
GEO. D. FULLER, *Assoc. Editor*

Report accepted in full.

REPORT OF THE BUSINESS MANAGER OF ECOLOGY

For the Fiscal Year, December 1, 1931–November 30, 1932

Received			
Cash on hand (Statement of 1931)		$ 399.55	
Raymond Kienholz, Treasurer, E. S. A.		2,170.05	
Subscriptions, 1932	$1,670.64		
Subscriptions, 1933	308.03		
		1,978.67	
Single Numbers and Back Volumes		392.05	
Contribution—Anonymous		343.18	
Interest, June, 1932, received from bank		3.14	
			$5,286.64
Disbursed			
Printing			
Lancaster Press, Inc.			
October, 1931, issue	$887.66		
January, 1932, issue	653.86		
April, 1932, issue	765.86		
July, 1932, issue	567.56		
		$2,874.94	
Illustrating			
National Engraving Co.			
October, 1931, issue	$129.60		
January, 1932, issue	73.47		
April, 1932, issue	86.59		
July, 1932, issue	77.55		
		367.21	
Advertising		105.68	
Office Expenses			
Clerical Asst. for 12 mo. @ $10.00	$120.00		
Stationery	7.00		
Wrapping Material (paper and twine)	2.48		
Postage	73.50		
Expressage	2.79		
		205.77	
Miscellaneous			
Refunds on Subscriptions	$5.45		
Tax on Checks	.22		
		5.67	
Balance, November 30, 1932		1,727.37	
			$5,286.64

Examined and found correct.
H. P. SHOENBERNER, *Auditor*

Assets and Liabilities

December 1, 1931–November 30, 1932

Assets

Cash in Bank			$1,727.37
Bills Receivable			
Back Volumes		$ 15.00	
Subscriptions, 1932	$ 7.95		
Subscriptions, 1933	156.93		
		164.88	
Single Numbers		2.30	
			182.18
			$1,909.55

Liabilities

Bills Payable			
Lancaster Press, Inc., October, 1932, issue	$656.70		
National Engraving Co.	84.26		
Brooklyn Botanic Garden	7.63		
Remington Rand	4.25		
		$ 752.84	
Assets over Liabilities		1,156.71	
			$1,909.55

Circulation Data as per Mailing List of October, 1932

1. Members	531
2. Subscribers	519
3. Exchanges	95
4. Advertisers	13
5. Editorial Office	2
	1,160
Number of copies printed per month	1,400

C. Stuart Gager,
Business Manager of Ecology

Report accepted and approved.

The meeting adjourned at 12:50 P.M.

Report of the Editor of Ecological Monographs

The following report was approved:

Gentlemen:

Following is the report for *Ecological Monographs* for Volume 2, published during the year 1932; 515 pages, 214 figures.

Expenditures		$3,365.65
Printing and binding	$3,305.65	
Postage	60.00	
Receipts		
Two hundred subscriptions		900.76
Deficit		$2,464.89

A. S. Pearse,
Editor

MEETING OF DECEMBER 29, 1932

The Society met at 11:50 A.M. with President Nichols presiding.

REPORT OF THE SECRETARY-TREASURER

The report of the Secretary-Treasurer was presented and approved as follows:

Receipts under A. E. Emerson

Balance on hand, December 1, 1931		$ 707.27
Dues 1931	$ 16.40	
1932	244.00	
Sustaining 1932	44.00	
Contributing	6.00	
		302.40
Total receipts, January 19, 1932		$1,009.67

Disbursements under A. E. Emerson

Ecology (memberships)		$441.40	
Ecological Monographs (memberships)		105.00	
Secretary's Office—Stamps	$ 3.64		
Clerical work	34.95		
		38.59	
Expenses of secretary, New Orleans		66.26	
Committee on "Preservation of Natural Conditions and Study of Plant and Animal Communities"		100.60	
Check returned		1.00	
Total disbursements, December 1, 1931–January 19, 1932			$ 752.85
Balance turned over to R. Kienholz			$ 256.82

Receipts under Raymond Kienholz

Balance on hand, January 19, 1931		$ 256.82
Dues—Current (1932)	$1,428.24	
Advance (1933)	702.00	
Arrears	32.68	
Sustaining (1932)	282.00	
Sustaining (1933)	186.00	
Contributing	25.00	
		2,656.52
Naturalists Guide Royalty		19.50
Refund		39.00
		$2,971.84

Disbursements under Raymond Kienholz

Ecology (memberships)		$1,718.95
Ecological Monographs (memberships)		235.00
Secretary's Office		
Postage, Telegrams and Express	$ 29.31	
Clerical Assistance	5.80	
Printing and Stationery	197.65	
		232.76

Committees on Preservation of Natural Conditions and Study of Plant and Animal Communities		71.71
Checks returned, exchange and tax on checks		9.04
Total		$2,267.46
Balance on hand		704.38
General Fund		
Cash on hand		$ 614.41
Life Membership Fund		
Cash on hand	$ 89.97	
Securities	1,120.63	
		$1,210.60

Membership—1932

Sustaining Life	2
Life and Sustaining	2
Life	7
Sustaining Institutional	3
Sustaining	82
Institutional	5
Active	432
Contributing	13
Associate	30
Total paid up	576
In arrears 1 year	85
Total	661

Raymond Kienholz, *Secretary-Treasurer*

On the recommendation of the President and approved by the Society, no action was taken on the Constitutional Amendment but a committee appointed consisting of W. C. Allee, G. D. Fuller, R. C. Osburn, and E. N. Transeau to revise Article 6 of the Constitution.

The resignation of Dr. A. S. Pearse as editor of Ecological Monographs necessitated the following report which was accepted and approved.

Report of Special Nominating Committee to Consider the Editorial Board of Ecological Monographs

The committee heartily recommends that the resignation of Professor A. S. Pearse as managing editor of *Ecological Monographs* should not be accepted.

We recommend the appointment of Dr. C. F. Korstian stationed at Duke University as associate editor and that Professor Korstian be given special duties with regard to the papers in Plant Ecology corresponding to the position held by Dr. G. D. Fuller on the editorial board of Ecology.

Since the provisions originally made for periodic consideration of this editorial board have not been carried out, we recommend:

First, that Drs. Juday and Transeau, whose terms expire this year, be continued in office one more year.

Second, that Drs. Coker and Gleason be appointed for a two year term ending in 1935, and

Third, that Drs. Kennedy and Cooper be appointed for the normal three year term.

All these recommendations are made not with the idea that these appointees will necessarily retire from the board at the close of their term but that their further continuation will be reconsidered at that time.

(Signed)

G. E. Nichols
W. C. Allee
G. D. Fuller
A. O. Weese

President Nichols reported on the proposed plans for the reorganization of the National Research Council and the response of past presidents of the Society relative to these plans. The Society endorsed his recommendations based on the returns from the past presidents and requested that the recommendations be sent to the National Research Council.

The following resolution was approved by the Society.

Institute of Forest Biology

The Ecological Society of America desires to emphasize the need for coordinated research in all phases of forestry and in the factors affecting the forest; not only trees, but associated herbaceous and shrubby vegetation, fungi, insects and other animals, soils and their organisms, and geological formations.

Fundamental research in forest biology, which requires funds to insure protracted investigations, can appropriately be conducted in institutes of forest biology. Such institutions have been recommended by a committee of the Society of American Foresters and by I. W. Bailey and H. A. Spoehr in " The Rôle of Research in the Development of Forestry in North America." The Society believes that the establishment of fully equipped and adequately financed research institutes of forest biology will greatly advance forestry in the United States and will contribute materially to the advancement of science.

The following officers were elected for the year 1933:

President—E. B. Powers,
Vice-president—H. C. Hanson,
Secretary-Treasurer—Raymond Kienholz.

The meeting adjourned at 12:30 P.M.

Raymond Kienholz, *Secretary*

NOTES AND COMMENT

TEMPORARY HIGH CARBON DIOXIDE CONTENT IN AN ALASKAN STREAM AT SUNSET[1]

In the summer of 1931 the author and his assistants witnessed a peculiar situation arise at sunset in a stream in southeastern Alaska. This stream is located on the eastern slope of a high mountain range that is snow capped the year round. The stream originates in a large mountain lake from which it flows over a series of falls with a total drop of 200 feet. From the foot of these falls it flows swiftly over shallow gravel beds and short rapids for approximately one and one-half miles and then empties abruptly into a deep pool at a sharp bend in its course. For a quarter of a mile below this deep pool, the stream becomes very sluggish, averages 4 to 6 feet in depth, and quietly flows over a sandy mud bottom. At the lower end of this comparatively quiet stretch, the stream again flows over swift rapids and then over a 10-foot falls into a shallow sandy lagoon. From this lagoon the water passes through a narrow rocky channel into the tide flats of the bay.

This stream, like many other streams of its size in Alaska, forms the spawning ground of a large run of pink salmon (*Onchorhynchus gorbuscha*) each summer. The pink salmon begin to enter the stream during the second week in July and, for the most part, school up in the stretch of comparatively quiet water just below the gravel beds. They move slowly about in this part of the stream until late in the summer before they become sexually mature and move up stream to spawn on the gravel beds. In the summer of 1931 approximately 80,000 pink salmon remained in this stretch of quiet water until late in August. The weather during the latter part of July of this year was cool and an abundance of rain kept the stream surging near the tops of its banks. However, during the first week in August the weather changed and became fair and warm. This brought a marked drop in the water level of the stream so that most of the water came from the melting snow in the mountains. The temperature of the stream increased from day to day and reached a maximum of 66° F. on August 5 and 6. On both of these days the air temperature reached a maximum of 90° F. Regardless of the high temperature and low water the school of 80,000 salmon milled about in their close quarters without any apparent discomfort. However, at sunset on August 6 and for approximately 30 minutes thereafter it seemed as though some immediate death dealing substance had been thrown into the stream. The salmon began to die by the hundreds and float down stream belly up and motionless. Not only the salmon but the trout and fresh-water bull heads in the stream shared the same fate. In their death throes the fish gave the appearance of suffering from suffocation. Approximately 5000 salmon and many other fish in this part of the stream perished at this time.

When the salmon in the quiet stretch began to die, one man was sent up stream to make observations at a point A on the gravel beds just above the sharp bend in the stream. Another man was sent to make observations at a point C in the deep pool just below the lower falls. Water samples were taken in the stream at point B where the fish were dying and at point C. When the observer who was sent up stream arrived at the upper end of the stretch of quiet water he found that the salmon were swarming out of it by the thousands and furiously beating their way up stream in the shallow water on the gravel beds. The observer who was sent down stream found that the 1000 or more salmon in the deep pool below the falls were milling about as usual and showed no signs of discomfort. The analysis of the water samples gave a clue to the situation. The pH

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[1] Published by permission of the Commissioner of Fisheries.

of the water in the stream at point B where the fish were dying was 5.6 at 65° F. whereas the pH of the water at point C below the falls was 6.1 at 65° F. The fixed carbonate content or the Bik. (Saunders, '26) of the water at points B and C was the same. Each sample of 100 cc. required 1.0 cc. of N/100 HCl for titration with methyl red indicator. The specific gravity of the water at points B and C was the same being 1.001 at 15° C. In fact, the chemical analysis of samples of water taken at point C on previous days was practically the same as that found on August 6.

At first the salmon in the quiet stretch of water died very rapidly, more of them seeming to perish in the lower end of the school than in the upper end where they were rapidly moving up on the gravel beds. This, however, did not continue, for the lethal effect of the water began to pass away and after a period of 30 minutes the remaining salmon began to mill about as before. A water sample was again taken in the stream at point B and the pH found to have risen to 6.0 at 65° F. Nothing has been mentioned concerning the atmospheric conditions during the catastrophy and herein may lie the explanation to the sudden death of so many apparently healthy fish.

When the sun sets in this part of the country it merely drops behind the high mountain range. Hence the sun can be throwing warm penetrating rays over the valley of the stream and within 15 minutes disappear behind the mountains. This is what took place at 6 o'clock on the evening of August 6. The air was exceptionally clear all through the day and the sun had no interference in sending its penetrating heat rays into all parts of the valley. In the evening when the sun sank behind the mountain range its penetrating heat rays seemed to stop short. The atmosphere at this time gave one a rather unusual feeling for everything was so still. No breeze was stirring and the air seemed to suddenly become cool. The atmosphere remained in this condition for a time and then a cool breeze came down the valley from the snow-capped peaks. After the breeze came up the lethal effects of the water began to wear off and the fish ceased dying in the stream.

Hazardous as this may seem, the author is of the opinion that the sudden stillness of the air formed a temporary blanket over the quiet stretch of water in the stream where the school of 80,000 salmon slowly milled about. In view of the low pH of the water in the stream at point B, this blanketing effect of the still air apparently caused a sudden rise in the carbon dioxide content of the water. This rise was sufficient to bring about the asphyxiation of the salmon and other fish that were milling about in the quiet stretch of water. Had the acidity of the water in the stream where the fish were dying been due to a substance other than the presence of carbon dioxide, then the pH of the water below the falls would likewise have been 5.6 at 65° F. However, this was not the case. No doubt the shaking up of the water as it swiftly moved over the rapids and falls removed its excess carbon dioxide content and likewise its lethal effects. Again when the air began to move in the valley over the stream and a large number of the salmon were well on their way up stream, the pH of the water at point B changed from 5.6 to 6.0. It was also at this time that the fish ceased to perish from suffocation. The large number of salmon that migrated up stream in the shallow water on the gravel beds showed no signs of becoming asphyxiated but on the contrary were very active. The 6 to 10 inches of water on the gravel beds was thrashed about so violently by the onrushing salmon that it was completely aerated regardless of the large number of salmon in it.

During the succeeding few days after the catastrophe the majority of the salmon gradually dropped back into the quiet stretch of the stream and remained there until later in the summer before starting their spawning migration. The weather changed on August 7 and thereafter so that this peculiar situation did not arise again during the remainder of the summer.

In the summer of 1932 observations were again made at sunset in this stream. The run of pink salmon in the stream, however, was much smaller than in 1931. Only approximately 10,000 pink salmon schooled up in the quiet stretch of the stream. From

August 14 to 25 the weather was fair and warm and the water level of the stream remained far below normal. Repeated analyses of the stream water at points B and C at sunset showed the pH to be 6.3 at 61° F. for both points in the stream.

Harvey ('28) has shown that the carbon dioxide pressure increases rapidly in a non-linear manner with a decrease in the pH in waters with low alkaline content. Since the Bik. of the water in the stream at Olive Cove is very low, the drop of .4 in the pH of the water at point B on August 6 was no doubt accompanied by a sudden increase in the carbon dioxide pressure. According to Saunders' ('26) formula the carbon dioxide pressure in the water at point B at pH 5.6 was approximately 50 per cent greater than the pressure when the pH was 6.0 Powers ('32) from his experimental work on the respiration of fish points out that an increased carbon dioxide pressure of the water will cause an increase in the acidity of the blood of the fish and in extreme cases cause a destruction of the red blood corpuscles in their blood vessels. It may be that the sudden change in the carbon dioxide pressure of the water in the stream in the region of point B caused a drastic change in the respiratory function of the fish which resulted in the sudden death of the salmon and other species of fish in that part of the stream.

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The Preservation of Natural Biotic Communities

A. Introduction

There appears to be a definite desire on the part of the people of all countries to preserve at least some of the original vegetation and wild animals. The national parks as well as other parks and reservations of Europe, Africa, the United States and Canada are well known examples. However, types of vegetation other than forest have usually not been preserved except incidentally as inclusions within the forested area or in connection with some historical and ethnological remains. The larger wild animals of all civilized countries have been greatly reduced in numbers, some because they are a hindrance to agriculture, others because of their value as food and clothing. Still others have been slaughtered for no good reason. Many people think that the national parks of Canada and the United States, some state and provincial parks, and some national forests have escaped this elimination of large animals. They believe that such areas are examples of primeval nature with the animal life essentially complete. The national parks of both countries doubtless represent the least disturbed series of areas which we have on the continent. Some state and provincial parks and one or two of the national forests in each country may be equally undisturbed at present, but probably less well safeguarded or on a less permanent basis. Yet, many have been surprised to learn of the large amount of modification which has gone on in times past within these park areas, both before and in some cases perhaps after they were set aside.

The whole trend of research and education is toward specialization on particular objects or particular organisms. These are stressed while the assemblage to which they belong is ignored or forgotten, together with the fact that they are to be regarded as integral parts of the system of nature. Outside of modern ecology and geography there has been little or no tendency towards the development of specialists on the entire life of natural areas. Perhaps one reason why nature study has been unsuccessful is because too often it is not the study of nature but of single natural objects or groups of objects which constitute a small part of any natural aggregation. Often this has resulted in the development of emotions relative to the plants or animals singled out for this study, followed by sentimental desires to protect them.

Biologists are beginning to realize that it is dangerous to tamper with nature by introducing plants and animals, or by destroying predatory animals or by pampering herbivores. Much of the so-called "control" of noxious insects, of predatory animals, and of plant diseases is based upon the idea that nature can be "improved." This is, of course, the dominant idea in all agricultural, silvicultural and game cultural practice. The fact remains, however, that wolves and other predators, and herbivores in numbers have lived together for thousands of years without disaster and that in some of our national parks they have lived together with far better maintenance of natural conditions than in areas where control has prevailed.

In general, from a philosophical and practical viewpoint, the unmodified assemblage of organisms is commonly more valuable than the isolated rare species. However, because the significance of the unmodified assemblage is popularly ignored, the whole is commonly sacrificed in the supposed interest of the rare species. Due to the local habitat relations of the rare species, neither need be sacrificed in any large natural area, hence the importance of large sanctuaries.

The principal activity of field ecologists might be stated to be the gathering of data for the interpretation of nature. To the ecologist, it is the entire series of plants and animals which live together in any community which is of primary interest.

The Ecological Society of America has always been interested in the preservation of natural areas with all their native animals. A committee composed of its members published a book entitled *The Naturalist Guide* ('25) listing a very large number of such areas and so is in position to know the extent and present condition of such areas. Only a very few were reported in a pristine condition so far as animals were concerned. The society has recently held a number of conferences with park and forest officials and after careful consideration, prepared the following memorandum dealing with (1) definition, (2) size, and (3) classification of natural areas containing original plant and animal life.

B. NATURE SANCTUARIES OR NATURE RESERVES

I. *Meaning and Use of the Term*

Just what original nature in any area was like from a biological viewpoint, is not known and never can be known with any great accuracy. Primitive man, who could not remove the forest or exterminate the animals, is probably properly called a part of nature. At the time of the discovery of America, a scattered population of Indians had locally modified the vegetation, but had not destroyed any of the vegetation types. However, most of the areas which are now available for reservation as nature sanctuaries or nature reserves were probably not much affected by these primitive men. This is the argument for leaving them out of the picture.

"Nature" and "natural" are purely relative terms and can have significance only as averages, because the outstanding phenomenon of biotic communities is fluctuations in numbers of constituent organisms or reproductive stages of organisms over a period of one to thirty or more years. Thus, a Nature Sanctuary is primarily an area in which these fluctuations are allowed free play.

The term *Nature Sanctuary* has been applied to areas covered by natural vegetation, but not containing all the animal species. In Europe, for example, in some of the nature parks no timber is removed and only persons with serious scientific or other scholarly interest are admitted. The Nature Sanctuaries are surrounded by areas in a less natural state, such as nearly natural forest devoted to growing timber, game production, etc. These surrounding lands are called *buffer* areas of partial protection.

In the United States and Canada areas of nearly natural vegetation are larger than in central Europe and fewer of the animals have been lost. It is possible, therefore, to recognize several classes of Nature Sanctuaries in North America.

II. *Classes of Nature Sanctuaries*

The categories below are arbitrary and merely for the purpose of providing provisional basis ranking of natural areas. The classification of each area should be determined by a committee of competent naturalists.

1. *First Class Nature Sanctuaries.*
   Any area of original vegetation, containing all the animal species historically known to have occurred in the area (except primitive man), and thought to be present in sufficient numbers to maintain themselves, is suitable for a first class Nature Sanctuary.
2. *Second Class Nature Sanctuaries.*
   - *A.* Second growth areas (of timber) approaching maturity, but conforming to the requirement of No. 1 in all other respects.
   - *B.* Areas of original vegetation from which not more than two important species of animal are missing.
3. *Third Class Nature Sanctuaries.*
   Areas modified more than those described under No. 2.

III. *Other Terms and Their Meanings in Common Usage*

1. *Nature Sanctuary*—This emphasizes not only the stationary (floral) elements but also the motile (faunal) elements. It necessitates buffering and noninterference by man.
2. The only synonym for Nature Sanctuary that has been suggested is *Nature Reserve.*
3. *Research Reserve* (U. S. National Park Service sense) means Nature Sanctuary, as the areas are selected to represent the primitive biological condition and admission is by permit only. The U. S. National Park Service appears to be working toward a three-zone plan: (*a*) a zone of development which is a small portion of the park devoted to hotels, camps, etc.; (*b*) the greater portion of the park open to the public and traversed by trails and roads (in many cases these areas may serve as second or third class Nature Sanctuaries); (*c*) Research Reserves open to the public only by permit.
4. *Natural Area* (U. S. Forest Service sense)—This emphasizes the stationary elements of nature, hence is primarily floral.
5. *Buffer Area* is a region surrounding a Nature Sanctuary in which the biotic community, especially the vegetation, is only slightly modified by man. It is a region of partial protection of nature and may be zoned to afford suitable range for roaming animals under full protection.
6. *Research and Experimental Area*—This usually implies modification and management of some of the biological elements.
7. *Primitive Area* (U. S. Forest Service sense)—This is defined as an area in which human transportation and conditions of living are kept primitive. Some of the areas are to be cut over periodically.
8. *Wilderness Area*—This is defined essentially as is *primitive area.*

IV. *Availability of Nature Sanctuaries and Buffer Areas in North America*

A. Nature Sanctuaries or Nature Reserves.

1. Except for Desert and Tundra areas, conditions suitable for first and sec-

ond class Nature Sanctuaries are available only in connection with National Parks and National Forests and (in rare instances) State Parks in the United States and in the National Parks and some Crown Lands and Provincial Forests and Parks in Canada.

2. In eastern North America few first class Nature Sanctuaries of national importance can be established because of the absence of the wolf, wapiti and some other species.
3. Status of Natural Areas in the U. S. National Forests. These have not been selected with consideration for animals. All are too small to contain roaming animals, but could suffice as Nature Sanctuaries, if necessary, when surrounded by high grade buffer areas in which the roaming animals are protected. To be of full value from the standpoint of primeval forest conditions and processes, all roaming animals must be allowed ingress, or abnormal conditions are likely to arise and defeat the purpose of the natural area from the standpoint of forestry.
4. Research Areas or Nature Sanctuaries in the National Parks. The remarks under No. 2 may possibly be applicable to the eastern National Parks.
5. State Parks, National Monuments (U. S.), private holdings, etc., will usually afford third class Nature Sanctuaries, but their maintenance in the condition in which found or with such improvements as may be possible, is all the more important.

B. Buffer Areas and Modified Sanctuaries in Different Biotic Types.

1. *Forested Areas.*
    - (*a*) Areas reserved for experimental work for which the Nature Sanctuary serves as a check (*e.g.*, in case of Experimental Forests).
    - (*b*) Areas devoted to recreation or serving as game refuges. (In the larger National, Provincial and State Parks and National, Provincial and State Forests.) There should be a zone of these types surrounding each Nature Sanctuary inside areas described under (*c*).
    - (*c*) Areas in which there has been selective cutting, grazing approaching capacity, etc.
2. *Woodland Areas.*
    - (*a*) Pinyon, Cedar, etc. The same principle holds as above.
3. *Scrub Areas.* Much scrub is said to have been produced by the invasion of grassland by shrubs belonging to arid or xeric areas through overgrazing. The herbs and grass of large areas of semi-desert scrub have been seriously damaged by over-grazing in western United States. Except in extreme desert these factors make the selection of scrub sanctuaries very difficult. Ideally, large modified areas should be fenced and allowed to return to the original condition while buffered by an area of restricted grazing.
4. *Grassland.* There are now natural areas of some types of grassland in the National Forests and Range Reserves or Experimental Ranges, but often these cannot be buffered and are usually too small and lack the original large animals. Ideally, large areas should be buffered by grazing and experimental areas.
5. *Semi-aquatic and Aquatic Areas.* The buffer area should consist of developmental stages of terrestrial vegetation as far as a late subclimax stage for the region.

V. *Size of Sanctuaries and Relations to National Parks and Forests*

1. The reserved areas in the National Parks are possibly too small, but in any event should be zoned about by (buffer) areas of complete or partial protection of the roaming animals. These zones of protection for certain animals would merely restrict occasional control measures to definite territory.
2. The forested natural areas in the National Forests are many of them too small and should be enlarged in some cases, but must in all cases be surrounded by zones of complete or partial protection for the large roaming animals.
3. Areas should not be fenced against any of the larger native animals, as their presence is necessary to make the conditions natural as regards vegetation, etc.
4. The Nature Sanctuary should be protected from fire, exotic organisms and diseases through management and preventive measures *within the buffer area.*
5. Size. The basis for size is purely biological and must be determined by biological conditions. The aims are (1) to preserve all the animals (birds, mammals and lower forms) native in the area and leave them to reproduce within the sanctuary entirely unmodified, and (2) to prevent tramping and other injury to the vegetation by man. The animals have to receive primary attention, but vegetation types must also be represented. Two types of sanctuary seem possible: 1. First class sanctuaries in which wolves, mountain lions, bob-cats, coyotes, and migratory game are to be protected, and 2. Second class sanctuaries in areas where these animals have been exterminated or never existed (especially in the smaller parks and forests).

(1) *First Class Sanctuaries and Buffer Zones for Animals*

The animals requiring first and most careful consideration are the carnivores, likely to be unpopular with the agricultural (broad sense including game culture) interests outside the park or forest.

The home range of these animals must be considered. That of the wolf is said to be 50 miles, the coyote 20 miles, the bob-cat 10 miles, and the mountain lion 20 miles. These animals are slated for general extermination by some sportsmen and can be held unmolested only in areas within the larger well-buffered parks or remote wilderness areas of the national forests.

A second group demanding careful study is the migratory herbivores. These in combination with the carnivores (wolf, bob-cat and puma) will give most of the difficulty in selecting nature sanctuaries. Each sanctuary will constitute a problem in itself.

The terrain must be selected with great care wherever choice is possible so as to be about equally favorable to all the native species. The area should also meet with approval as a plant ecological reserve. Areas suitable for all the larger animals should be selected in the large parks, notably McKinley, Yellowstone, Yosemite, Grand Canyon, Rainier, etc., in the United States and Mt. Robson, Jasper, Rocky Mt., Strathcona, Algonquin, Quetico, etc., in Canada.

In so far as possible natural topography should be utilized to bound areas. Places remote from tourist travel without approach by roads or trails may be suitable without guards, but frequently some kind of guarding will be necessary. Each area will prove different in the problems encountered.

The sanctuaries may well be surrounded by areas in which there is some visitation by a limited number of persons; each park will again be a special problem.

(2) *Second and Third Class Sanctuaries*

The same principles hold for the smaller sanctuaries as for the large ones, but the problems are much less difficult, because the larger animals cannot be given any special attention. They may be established in parks and forests of various types, but within the small state parks and reserves there can never be true Nature Sanctuaries because of the lack of the large animals.

(*Notes:* 1. It is necessary to recognize that the National Park Service is under some pressure to let everyone go anywhere in a national park.

2. The game of the U. S. National Forests, including that in the Primitive areas and Natural areas, *belongs to the state in which the forest* is located and is subject to trapping in some cases and to state predatory animal control in others. This is the greatest difficulty in making first class Nature Sanctuaries of the National Forest Natural areas. It will probably take some time to clear this up, either through the states or the federal government. Members of the Ecological Society should use every means to educate the public as to the value of sanctuaries so as to reduce and eliminate these difficulties.)

C. Methods of Securing the Establishment of Nature Sanctuaries

1. The first principle is to point out the need of complete Nature Sanctuaries. They are essential if any of the original nature (broad sense including large animals) in North America is to be saved for future generations for scientific observation of the important phenomenon of fluctuations in abundance of plant and animals, their social life, etc.

2. Due to our lack of knowledge of these fluctuations, each change in abundance is viewed with alarm by custodians. Hence, constant pressure must be exerted on governmental agencies to prevent the current popular ideas relative to "control," "modification," and "improvement," of natural areas from affecting national parks, provincial and state parks and other reserves containing natural areas suitable as nature sanctuaries and with buffer territory.

(*a*) Facts now available indicate that many of the control measures have been useless because they were applied to animals at their maximum abundance and only hastened the natural decline.

(*b*) The experiment of letting areas essentially alone, so successful in a few of our parks, is worthy of repetition. Many of the areas within which nature sanctuaries and buffer areas may be established have already been modified, but remedial measures directed toward the return to a so-called equilibrium consist chiefly in allowing nature to take its course. Any other measure should be undertaken only after the most careful consideration.

3. This Committee of the Ecological Society urges a sub-division of all but the smaller reserves into (1) sanctuary, (2) buffer area of partial protection, and (3) area of development for human use where this is one of the aims of the reserve. It further urges that these three sub-divisions be so arranged as to give best conditions for roaming animals within the buffer area and the sanctuary.

4. The aim of the Ecological Society of America and cooperating societies is to secure adequate scientific observation bearing on these fluctuations in abundance and other phenomena which will be furthered by skilled watching of the natural course of events in these reserves.

5. They further aim to stimulate cooperation between the controlling agencies in charge of game and vegetation reservations and in nature sanctuaries and buffer areas in order that more logical units be developed and better methods of administration be obtained.

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AFRICAN BIRD DISTRIBUTION IN RELATION TO TEMPERATURE AND RAINFALL

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The peculiarly uneven distribution of rainfall over the continent of Africa has served, to a large extent, to divert attention from temperature as a factor of importance in influencing avifaunal distribution in the Ethiopian Zoogeographical Region.[1] Africa, unlike other regions, possesses no well-defined mountain system which might serve to focus attention on the temperature factor. The influence of the higher mountain peaks upon its avifauna is of relatively minor importance, due, no doubt, to the isolation and small extent of these mountains. The broad expanse of plateau-like highlands which extends from Abyssinia south to the Cape, with a branch running westward to Angola, is relatively too low to induce any very striking reaction on the part of the avifauna. Nevertheless, this highland system plays a fundamental part in its effect on bird distribution.

The concentration of forests, and richly vegetated lands, in western equatorial Africa, as a result of the generally heavier precipitation there, and the development of the vegetation of the remainder of the continent in a series of concentric semi-circles, or belts, of progressing aridity around this center, has had a remarkable effect on avifaunal distribution. The occurrence within this central area of many genera and species of birds not found elsewhere has led to the differentiation, by zoogeographers (Wallace, '76; Reichenow, '01; Chapin, '23), of a "West African Subregion" distinct from the remainder of the region. The differences between these two subregions can, however, be shown, by analysis of the avifauna, to be due chiefly to the preponderance of forest-inhabiting genera and species in the one, and to an abundance of plains and semi-desert forms in the other. The distinction is, thus, a quantitative, more than a qualitative one.

Were the rainfall of Africa more evenly distributed, as in other parts of the world, concentration of the forests into a single central area would not occur, and a primary zoogeographical division into subregions characterized

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[1] Africa, south of the Sahara, and southern Arabia. Madagascar is included by some as a subregion, while, by others, it is made a distinct region.

by contrasting types of habitat could not be made. The occurrence, moreover, of a few scattered forest patches (owing to the influence of local topography on the rainfall) beyond the limits of equatorial West Africa, and the presence in them of forest forms, some of which are closely allied, if not identical with those of the West African forests, lends support to the contention that Africa does not differ fundamentally from other regions of the world in regard to the factors controlling avifaunal distribution.

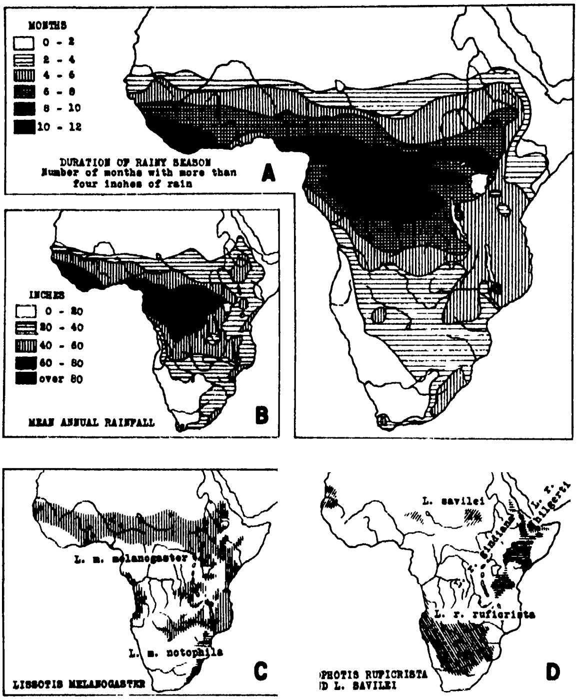

FIG. 1. Temperature in relation to African bird distribution

A. Mean annual temperature in ° F., drawn from data published by Knox ('11), Egyptian Physical Department ('22), Statham ('22), Fairweather ('25), and Brown and Brown ('30). Black dots indicate locations of weather stations. *B*. Köppen's ('00) classification of climate, based on types of vegetation. *C*. Distribution of *Calopelia* (black dots), a monotypic genus of forest doves with two subspecies confined to the Tropical Zone. Forested areas with a mean temperature over 70° F., and a rainfall over 70 inches, are indicated by vertical shading; those with a rainfall of less than 70 inches, by horizontal shading. *D*. Distribution of *Aplopelia* (black dots), a Subtropical Zone genus of forest doves with two species and several races. Forested areas with a mean temperature under 73° F., and a rainfall over 60 inches are indicated by vertical shading; those with a rainfall of less than 60 inches by horizontal shading.

The importance of temperature as a factor influencing the distribution of bird life in the Ethiopian Region has been discussed elsewhere (Bowen, '32). Certain climatological and other evidence was there presented to demonstrate the existence in Africa of temperature zones, comparable with those of the other zoogeographic regions. The extent of these is shown in the accompanying isothermal map (fig. 1, map *A*). The distribution of many Ethiopian birds may be explained largely by reference to these zones; but an understanding of the distribution of rainfall (fig. 2, map *B*), which is, in the main, the controlling factor governing the quantitative distribution of the vegetation (fig. 3, maps *A* and *B*), is necessary in order to explain peculiarities in the distribution of others. A few examples will illustrate:

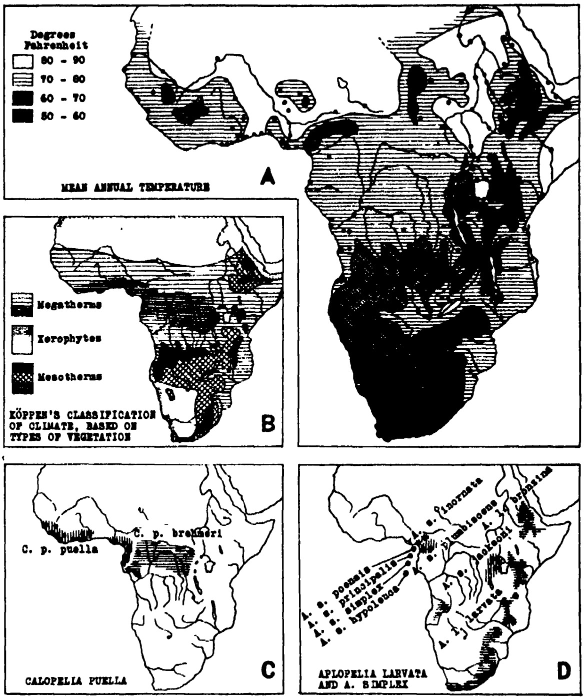

FIG. 2. Rainfall in relation to African bird distribution

A. Duration of rainy season. Number of months with more than four inches of mean rainfall (compiled from monthly rainfall maps by Knox, '11). *B*. Mean annual rainfall in inches (after Knox). *C*. Distribution of *Lissotis melanogaster* (black dots), a species of bustard characteristic of the drier savannas of the Tropical Zone. All areas with mean temperature over 70° F. and a rainfall of 20 to 60 inches are shaded. *D*. Distribution of *Lophotis* (black dots), a genus of bustards inhabiting arid areas with moderately cool temperatures. All areas with mean temperature 60° to 80° F. and a rainfall of less than 30 inches are shaded. *L. savilei* has been recorded from Senegal, but no specimen has been taken.

A small forest dove, belonging to the monotypic genus *Calopelia* (fig. 1, map *C*), occurs throughout the Guinean forests. Two subspecies are recognized. One, *C. puella puella*, is confined to the coastal forests of Guinea, where the total annual rainfall exceeds seventy inches; the other, *C. p. breh-*

meri, ranges throughout the Congo forests, where the rainfall varies from about sixty to seventy inches annually. The species is distributed only within the tropical zone (between the isotherms of 70° and 80° F.), notwithstanding the fact that in several places in the eastern Belgian Congo the forests of this zone are contiguous with those of the subtropical zone. Another, rather closely related genus of doves, *Aplopelia* (fig. 1, map *D*), is distributed in forests, wherever the mean annual temperature does not exceed 73° or 74° F. Two species are recognized. One, *larvata* (with *bronzina,* a race), is found throughout the forest patches of the subtropical zone, wherever the rainfall does not exceed 60 inches annually; the other, *simplex* (with

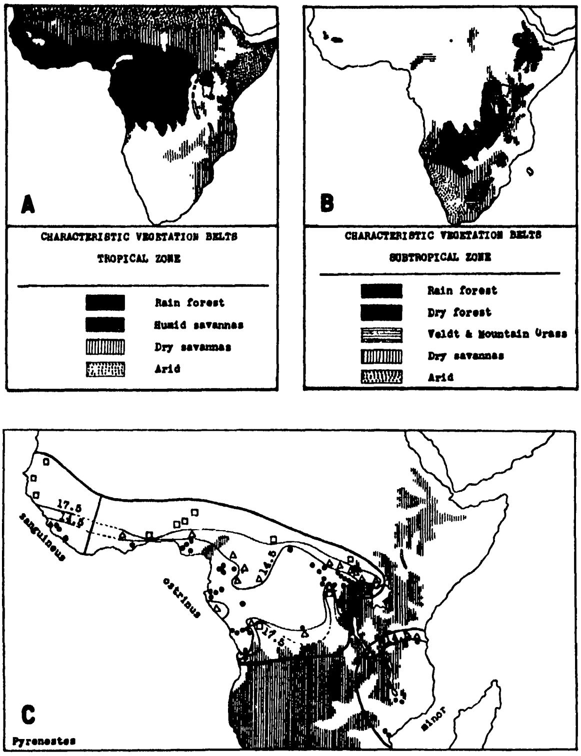

FIG. 3. Vegetation in relation to African bird distribution

A. Characteristic vegetation belts of the Tropical Zone (after Shantz). *B.* Characteristic vegetation belts of the Subtropical Zone (after Shantz). *C.* Geographical variation in *Pyrenestes,* a genus of weaver-finches, showing a correlation between the size of the beak and the character of the vegetation. Portion of a map by Chapin ('24) superimposed on a life-zone map (Subtropical Zone shaded) to illustrate the part played by temperature as a factor limiting the range of the genus. Points where birds occur with mandible averaging less than 14.5 mm. wide are marked with a round dot. Triangles indicate localities for specimens with beak from 14.5 to 17.4 mm. wide, and squares those of 17.5 mm. or over. Most of the known occurrences are represented.

several races), occurs in the areas of heavier precipitation (over 60 inches annually).

By way of contrast, our next examples may be selected from a family of plains-dwelling birds. The small, black-bellied bustards of the genus *Lissotis* consist of two species, one of which, *hartlaubi,* is found only in the Somali arid districts, and neighboring parts of the tropical zone, while the other, *melanogaster* (fig. 2, map *C*), ranges throughout the drier savannas of the tropical zone. Its range may, in fact, be outlined with fair accuracy by subtracting from that part of Africa with a mean annual temperature above 70° F., all the areas with a mean annual rainfall of more than 60, and less than 20 inches. The nearly related bustard genus, *Lophotis,* with two, or three species, has a distribution which is peculiarly discontinuous. On plotting its range, however, it appears that this genus inhabits only such areas as have a mean annual temperature of 60° to 80° F., and an annual rainfall not

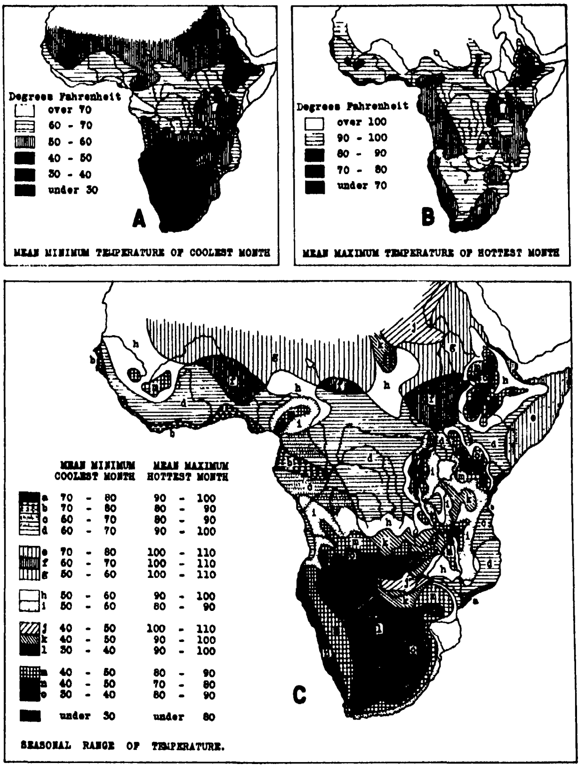

FIG. 4. Normal extremes of temperature

A. Mean minimum temperature of the coolest month in ° F. *B.* Mean maximum temperature of the hottest month in ° F. *C.* Seasonal range of temperature. Data used in compiling these maps were obtained from the same sources as those used in fig. 1, map *A*.

exceeding about 30 inches. If on a map of Africa all territory which does not fulfill these requirements is excluded, it will be found that, apart from the recorded localities of the species, as shown on the accompanying map (fig. 2, map *D*), Senegal, and a portion of northern Nigeria, are the only remaining suitable territories in which the genus might be expected to occur. *L. savilei* has, in fact, been recorded from Senegal (Bannerman, '31), although no specimen has yet been collected.

Perhaps one of the most interesting examples of the relation of bird distribution to rainfall is afforded by the genus *Pyrenestes,* a weaver-finch. Chapin ('24) has discussed this case at some length. He concludes that, whereas the color differences which distinguish the three species are probably due to isolation, the subspecific differences, exhibited chiefly by variation in the size of the bill, show a close correlation to the amount of rainfall. Indeed, he writes that "the average size of the birds' bills in any locality can be shown to give a rough index of the nature of the vegetation, or of the rainfall. . . . It seems likely that a correlation exists between the greater size of the bill and a more restricted diet of hard seeds of certain sedges." Chapin rightly concludes that altitude (or temperature) can have no relation to these subspecific differences; but it may here be pointed out that altitude seems to be a limiting factor, in so far as the range of the genus is concerned. Regarding *P. minor* little is known, but it seems not unlikely that it will prove to be a bird entirely of the tropical zone, just as *P. ostrinus* and *P. sanguineus* most certainly are. In the accompanying map (fig. 3, map *C*) one of Dr. Chapin's distribution maps has been superimposed upon a life-zone map, in order to show the limitation of the range of the genus to the tropical zone.

NATURE OF ZONAL BOUNDARIES

The mean annual isotherms of 20° C. (68° F.) have been suggested by Supan ('96) as the limits of the hot belt, or tropical zone. These coincide approximately with the polar limits of the trade-winds, and with the natural distribution of palms. Miller ('31) considers that these isotherms form a very convenient boundary, although their advantages are coincidental rather than causal. "In Supan's zones" this authority writes "we have a convenient framework with a real biological significance, into which a classification might be fitted. On closer inspection, however, the mean annual isotherm of 70° is an even better limit for the hot climates in many places. . . ." In the accompanying isothermal map (fig. 1, map *A*) the limits of this hot, or tropical zone are indicated by the unshaded, and lightly shaded areas.

The isotherm of 70° F., it will be seen, enters Africa at a point a little south of Durban, and, skirting the foothills of the Drakensberg Mountains, follows a northerly course as far as the Limpopo River, where it bends westwards to include the major part of the valley of that river. In Southern Rhodesia it follows the 2,000 or 3,000 foot contour, turning westwards to include almost the entire Zambesi Valley. North of the Zambesi, this isotherm follows approximately the 4,000 foot contour in Nyasaland, Northern Rhodesia, and the Katanga district of the Belgian Congo. In Angola, owing to the cooling effect of the Benguella Current, it descends, in the north, to about the 3,000 foot level, and along the coast to sea-level in the vicinity of Benguella. Still farther north, in Tanganyika Territory, this isotherm agrees with a contour of slightly more than 4,000 feet, while in Kenya Colony, Uganda, and the eastern Belgian Congo it approximates the 5,000 foot level. In Abyssinia it reappears at about 6,000 or 7,000 feet, while in central Darfur it follows the 4,000 or 5,000 foot contour. In Cameroon, this isotherm again appears, following now a contour of slightly less than 3,000 feet. Farther west, in the Fouta Jalon highlands of French Guinea, it unquestionably reappears, but temperature data from these highlands are not available.

Adopting the isotherms of 68° F. and 50° F., which Supan selected as the limits of the tropical and temperate zones, Köppen ('84) proposed temperature belts as follows: (1) a tropical belt, with all months above 68° F.; (2) a subtropical belt, with 4 to 11 months above 68° and 1 to 8 months between 50° and 68° F.; (3) a temperate belt, with 4 to 12 months between 50° and 68° F. Merriam ('94), after plotting the distribution of various animals in North America, utilized the idea of "summing" the mean daily temperatures, and, finding that isotherms so obtained coincided with the distribution of various forms of life, proposed two temperature laws. Briefly, he concluded that the factor limiting the northward distribution of life is the total quantity of heat available during the period of growth and reproduction (*i.e.*, the summer), while to the southward (*i.e.*, towards the equator) the mean temperature during the hottest period is the critical factor. Both Köppen's and Merriam's zones are based, thus, largely upon the idea that the quantity of heat during a given time is of greatest importance.

Merriam's life-zones, although accepted by many students of American mammals and birds, have been criticized by others, chiefly ecologists. Quite recently, Kendeigh ('32), after exhaustive studies on the temperature of the House-wren, and other North American birds, both in the laboratory and in the field, has expressed the belief that extremes of temperature are probably of more importance than is the quantity of heat during a given season. This author concludes that birds have "upper limits of temperature tolerance as well as lower limits, and these are effective in controlling distribution." If this is true in the climate of North America, where the seasons are sharply defined and the summers often but little longer than is necessary for the successful rearing of offspring, then how much more will it apply in the climate of Africa, where the seasons are ill-defined, and the lengths of the summers sufficient for the needs of reproduction.

The isotherms of the mean minimum temperature of the coolest month (fig. 4, map *A*) and the mean maximum of the hottest month (fig. 4, map *B*) are here selected as useful indices of the extremes of seasonal temperature. They represent the normal range of annual temperature to which a given organism must subject itself if it is to reside permanently in a given locality.[2] Examination of these two maps reveals several interesting facts. For example, the isotherm of 50° mean minimum of the coolest month coincides closely with the mean annual isotherm of 70°; but the zone of the highest mean minimum temperature (*i.e.*, 60° to over 70°) agrees, not with the zone of the highest mean annual temperature, but rather with that of less intense heat (70° to 80°). The zone of the highest mean maximum temperature of the hottest month (over 100°), on the other hand, coincides with the zone of the highest mean annual temperature; but the lowest maxima of the hottest month are found chiefly in the coastal regions and in the highlands: the greater part of the interior of the continent lying within the isotherms of 90° and 100° F., mean maximum of hottest month. Several distinct classes of temperature environment are thus apparent.

By combining these two maps we obtain a classification of the continent into areas differing, one from the other both in regard to the amount of heat and to the seasonal range of temperature (fig. 4, map *C*). These areas fall naturally into six categories, as follows:

(*a*) A hot belt (minimum temperature of coolest month never under 60° F.) with a seasonal range of temperature not exceeding 30°, and the maximum temperature of the hottest month never over 100° (horizontal shading on map).

(*b*) A hot belt (minimum temperature of coolest month never under 50° F.) with a seasonal range exceeding 30°, and the maximum of the hottest month always over 100° (vertical shading on map).

(*c*) An intermediate or transition belt (minimum temperature of coolest month 50° to 60° F.) with a seasonal range of 30° to 40°, and the maximum of the hottest month 80° to 100° (unshaded, and stippled on map).

(*d*) A cool belt (minimum temperature of coolest month under 50° F.) with a seasonal range exceeding 50°, and the maximum of the hottest month always over 90° (diagonal shading on map).

(*e*) A cool belt (minimum temperature of coolest month under 50° F.) with a seasonal range not exceeding 50°, and the maximum of the hottest month never over 90° (cross shading on map).

(*f*) A temperate belt (minimum temperature of coolest month under 30° F.) with a seasonal range not exceeding 50°, and the maximum of the hottest month never over 80° (solid black on map).

Ecological Divisions of the Ethiopian Zoogeographical Region

Next to temperature, rainfall appears to exert the greatest influence upon bird distribution in Africa. Unlike temperature, however, whose effect is as-

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[2] By migration, which is so highly developed in birds, many species contrive to live, during favorable seasons, in areas where their existence throughout the year would be impossible. In discussing zoogeography such species must be considered independently. The present paper is concerned only with the distribution, and reaction to environment, of such species of birds as are permanent residents or, at most, are given to wander no more than is necessary to obtain sufficient food during periods of scarcity.

sumed to be mainly direct, rainfall appears to affect bird distribution chiefly through its influence upon the vegetation. The character and abundance of plant life are largely determined by the amount of precipitation, but the duration of the rainy season is, perhaps, of even greater importance. Heavy precipitation over a short period is of less use to plant life in general than is a lighter precipitation covering more months of the year. Comparison of a mean annual rainfall map (fig. 2, map *B*) and one showing the duration of the rainy season (fig. 2, map *A*) with a vegetation map (fig. 3, maps *A* and *B*) illustrates this point. It will be seen that a mean precipitation of over 4 inches during a period of more than eight months is usually needed to support a vegetation of unbroken forest. Areas in which a mean rainfall of 4 inches or more, occurs during a period of 2 to 6 months only, the remainder of the year being usually entirely dry, may support a luxuriant growth of tall grasses and acacias during the wet season only. For the remainder of the year, these grassy savannas become more and more dry until, in most cases, they are burned over by the natives.

Grass fires, which are of regular occurrence over most of the African savannas, undoubtedly play an important part in influencing both plant and animal distribution. Ground-nesting birds in particular, must regulate their breeding activities as much in accordance with the periodic recurrence of fires, as with the seasonal cycle of rainfall. Insect life, perhaps the chief food source of most savanna birds, is driven off or destroyed by these fires and, for a period of varying length, these savannas become little more than a charred wilderness with scarcely a trace of food or cover for the avifauna. Areas with less than two months of rainfall exceeding 4 inches per month support, usually, little more than a scanty covering of scrub and desert grass. These areas are inhabited by a fauna which must needs be highly specialized for such arid conditions.

Köppen ('00) has published a map of the climates of the world, based chiefly on the character of the vegetation. In so far as now concerns us, he recognizes three climatic types in Africa, characterized by the nature of the vegetation (fig. 1, map *B*), thus: (*a*) *Megatherms*—plants which need continuously high temperatures, without much annual range (no cool season, the temperature of the coolest month over 64.5° F.) and also abundant moisture (with at least one month of heavy rain); (*b*) *Xerophytes*—plants which like dryness, and need high temperatures; (*c*) *Mesotherms*—plants which need moderate heat (59° to 68° F.) and a moderate amount of moisture.

Besides the amount of rainfall and its duration, the seasonal coincidence of temperature and rainfall cycles must be considered. Miller ('31) classifies the African climate as follows:

A. Hot climate (mean annual temperature more than 70° F.).
  1. Equatorial (double maximum of rains).
  2. Tropical marine (no real dry season).
  3. Tropical continental (summer rain).

B. Warm temperate, or subtropical (no cold season, *i.e.*, in no month below 43° F.).
1. With winter rain.
2. With uniform rain.

C. Hot deserts.

The map which accompanies this classification, however, shows far too restricted an area with mean annual temperature below 70° F.

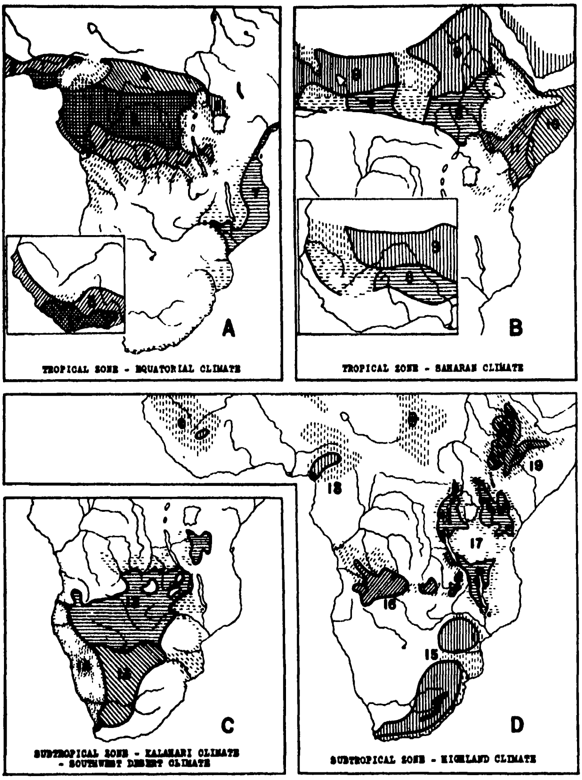

FIG. 5. Ecological divisions of the Ethiopian Region

The Tropical Zone exhibits two distinct types of climate: an Equatorial (map *A*) and a Saharan (map *B*). The Subtropical Zone is divisible into three climatic types: a Kalaharian and a Southwest Desert (map *C*) and a Highland (map *D*). Intermediate or transition areas, in which both Tropical and Subtropical Zone species may occur, are indicated by broken shading. The Temperate and Alpine Zones are indicated by the solid black areas on map *D*. Further subdivisions into Provinces and Districts (numbered consecutively on maps) are explained in the text.

Apart from temperature and rainfall, other factors undoubtedly play a part in influencing bird distribution. Among these, humidity, character of soil, and atmospheric pressure may be mentioned. The last named is probably a factor of some importance in limiting the distribution of a large part of the montane avifauna. The absence of some subtropical zone species of birds from the southern parts of this zone may be due to this factor.

In the accompanying maps (fig. 5) an attempt has been made to correlate these various factors, and to divide the Ethiopian Region into districts characterized by approximately uniform conditions of environment. Particular attention has been paid to the avifaunal map of Chapin ('23) since it is based primarily on the distribution of a large number of species of birds. In most cases a close agreement has been found between these environmental districts and Chapin's avifaunal districts, and the same names have been used. Some of these districts appear to be capable of further subdivision into areas which probably would be equivalent to the "Biotic Areas" of Dice ('22). For the present, however, it seems advisable to carry division no farther than to dis-

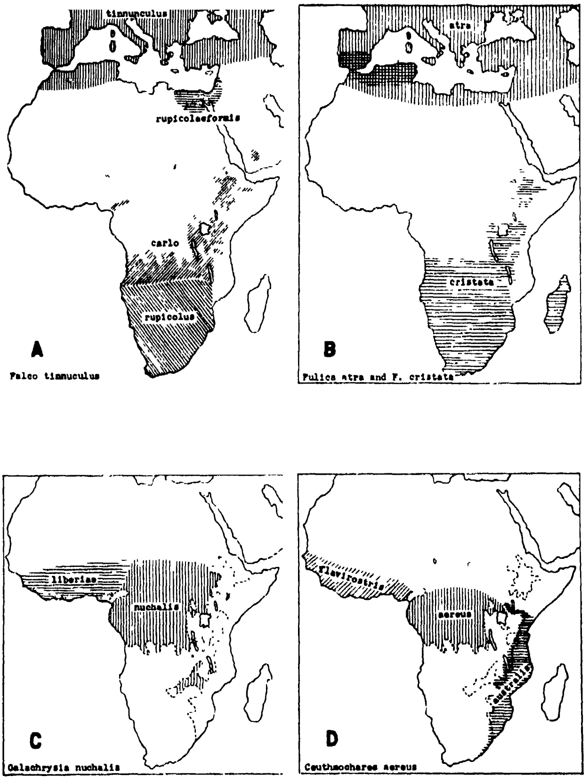

Fig. 6. Zonal distribution and the relation between the Palaearctic Region and the Subtropical Zone of the Ethiopian Region.

A, Falco tinnunculus, a kestrel common to the Palaearctic and the Subtropical Zone of the Ethiopian region; *B, Fulica atra*, the European Coot, and its African representative *F. cristata*, which is found only in the Subtropical Zone and a small part of the Palaearctic Region; *C, Galachrysia nuchalis*, the White-collared Pratincole, a river bird, chiefly of the West African Province of the Tropical Zone; *D, Ceuthmochares aereus*, a coucal found in the light forests and gallery forests throughout the Tropical Zone.

tricts until a complete analysis of the avifauna has been made. The nineteen districts here recognized may be classified as follows:

A. TROPICAL ZONE. Mean annual temperature over 70° F.; mean minimum temperature of the coolest month over 50° F.

- *a*. EQUATORIAL CLIMATE (fig. 5, map *A*). Temperatures high, but with little seasonal range (less than 30°). Mean annual temperature 70° to 80° F.; mean minimum of coolest month over 60° F.; mean maximum of hottest month under 100° F. Mean annual rainfall over 20 inches; more than 4 months with a mean precipitation over 4 inches.[3]
  - I. *West African Province* (West African Subregion of others). Mean annual rainfall over 50 inches; more than 6 months with a mean precipitation over 4 inches.
    - 1. Upper Guinea Forest District.
    - 2. Lower Guinea Forest District.
    - 3. Upper Guinea Savanna District.
    - 4. Ubangi Savanna District.
    - 5. Uganda Savanna District.
    - 6. South Congo Savanna District.
  - II. *East Coast Province*. Mean annual rainfall seldom over 60 inches; less than 6 months with a mean precipitation over 4 inches.
    - 7. East African Lowland District.
- *b*. SAHARAN CLIMATE (fig. 5, map *B*). Temperatures high and with wide seasonal range (over 30°). Mean annual temperature mostly over 80° F.; mean minimum of coolest month mostly under 60° F.; mean maximum of hottest month mostly over 100° F. Mean annual rainfall under 40 inches; usually less than 6 months with a mean precipitation over 4 inches.
  - III. *Sudanese Province*. Annual range of temperature over 40° F.
    - 8. Sudanese Savanna District.[4]
    - 9. Sudanese Arid District.[4]
  - IV. *Somalian Province*. Annual range of temperature 30° to 40° F.
    - 10. Somali Arid District.
    - 11. North Kenya Savanna District.[5]

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[3] The northern and eastern portions of Kenya Colony, and the northern coastlands of Angola, are here excluded on account of their aridity.

[4] Both these districts, which are really nothing more than vegetation belts, consist of alternating portions of true tropical arid climate, and portions of the Transition Zone (fig. 4, map *C*). Lynes ('25) has already called attention to changes from west to east in the avifaunas of these two belts, which cannot be explained by rainfall.

[5] This division of the single Somali Arid District of Chapin's map is tentative. The differences in both temperature and rainfall are about as great as those between the Sudanese Savanna and Arid Districts, and differences in the avifaunas of the two are found, but their numerical degree has not yet been ascertained.

B. TRANSITION ZONE. The territories in which the mean minimum temperature of the coolest month ranges from 50° to 60° F., and the mean maximum of the hottest month from 80° to 100° F., are intermediate in many respects between the Tropical and Subtropical Zones. Few if any birds are characteristic of this intermediate zone, but many species of the Tropical Zone occur here alongside others characteristic of the Subtropical Zone. This zone is indicated by the unshaded and stippled areas in fig. 4, map *C*, and by broken shading in fig. 5.

C. SUBTROPICAL ZONE. Mean annual temperature under 70° F. (except in the upper Zambesi Valley, where it goes as high as 80°); mean minimum temperature of the coolest month between 30° and 50° F.

c. KALAHARI CLIMATE (fig. 5, map *C*). Temperatures low, but with wide seasonal range (over 50°). Mean annual temperature 60° to 80° F.; mean minimum of coolest month 30° to 50° F.; mean maximum of hottest month 90° to to 100° F., or a little more. Mean annual rainfall less than 50 inches; less than 6 months with a mean precipitation over 4 inches.

12. Rhodesian Savanna District.[6]
13. Kalahari Arid District.

d. SOUTHWEST DESERT CLIMATE (fig. 5, map *C*, stippled). Temperatures low, and with little seasonal range (30° to 40° F.). Mean annual temperature 55° to 65° F.; mean minimum of coolest month 40° to 50° F.; mean maximum of hottest month under 90° F. Mean annual rainfall less than 20 inches: never as many as two months with a mean precipitation over 4 inches.

14. Damara Arid District.[7]

[6] Chapin's Angolan Highland District is, I believe, divisible into two, both in regard to climate and avifauna. The Angolan Highland District (16) is here restricted to the highest parts of Angola and the Katanga, which have a climate and an avifauna rather similar to those of the East African Highland District. The Rhodesian Savanna District might, on climate, be further subdivided, but a careful study of its avifauna will be necessary in order to determine whether or not it should be divided faunally.

[7] The Southwest Arid District of Chapin's map includes not only this, and the Kalahari Arid District, but also the southern part of the Rhodesian Savanna District. The distinction between the Kalahari and Southwest Desert Climates rests on differences in both temperature and rainfall; although in the extreme south, where there are less than two months with a mean precipitation over four inches, temperature alone is the differentiating factor. In a recent expedition to Southwest Africa, DeSchauensee ('32) encountered a change in the avifauna (mostly subspecific) soon after crossing the Orange River. This he was unable to account for by any differences in the amount of rainfall. Consulting the map of his route we find, however, that immediately after crossing that river he proceeded westwards, and soon entered the Southwest Desert Climate. The change noted in the avifauna was, I believe, due to this change in climatic (temperature)

e. Highland Climate (fig. 5, map *D*). Temperatures low, and with moderate seasonal range (40° to 50°). Mean annual temperature 50° to 70° F.; mean minimum of coolest month 30° to 50° F.; mean maximum of hottest month 80° to 90° F. Rainfall variable locally, usually not excessive.

- I. *Southeastern Province.*
    - 15. Southeast Veldt District.
- II. *Equatorial or Cameroonian Province.*
    - 16. Angolan Highland District.
    - 17. East African Highland District.
    - 18. Cameroonian Highland District.
- III. *Northeastern Province.*
    - 19. Abyssinian Highland District.

D. TEMPERATE ZONE.[8]

E. ALPINE ZONE.[8]

Relation between the Ethiopian and Palaearctic Regions

Besides the many Palaearctic birds that migrate to spend their winters in the Ethiopian Region, there is a number of forms common to both these regions. Some, obviously, have spread merely a trifle beyond the usually assigned boundary between the two regions. The occurrence of the Rock-Dove (*Columba livia*) in Senegal and the northern Sudan may be cited as an example. By far the greatest number of forms common to both regions are, however, wide-ranging species whose temperature requirements often seem as catholic as their ranges are wide.

There is still another group of birds common to both these regions, whose distribution is of particular interest, especially because it throws light on the temperature relations of the two. The Kestrel (*Falco tinnunculus*, fig. 6, map *A*), the Coot (*Fulica atra* and *F. cristata*, fig. 6, map *B*), the White-bellied Swift (*Micropus melba*, fig. 7, map *A*), and the Wryneck (*Jynx torquilla* and *J. ruficollis*, fig. 7, map *B*) may be given as examples.[9] In these

conditions. Farther north, at about Rehoboth, another, and more marked, change in the avifauna was encountered. At about this point he passed from the Damara Arid District to the Kalahari Arid District, and here both temperature and rainfall contribute to the distinctness of the two. Still farther north, at points just south of Lake Ngami and the Etosha Pan, yet another change in the bird life was observed. At both these points he entered the Rhodesian Savanna District.

[8] Both these zones are restricted to the upper levels of isolated mountain tops (indicated approximately by the solid black areas on map *D*, fig. 5). An account of their altitudinal limits, flora, and fauna is given by Chapin ('23).

[9] All the examples cited in this paper are selected from the non-passerine families. This is because my systematic studies of African birds in the museum of the Academy of Natural Sciences of Philadelphia have so far been concentrated chiefly upon these families. That the principle of zonal distribution holds equally in the passerine and non-passerine

cases the absence of the birds, either wholly, or to a large extent, as breeding residents within the limits of the Tropical Zone indicates a definite selectivity in regard to temperature conditions, and a climatic similarity between the Subtropical Zone of the Ethiopian and the Mediterranean districts of the Palaearctic Region.

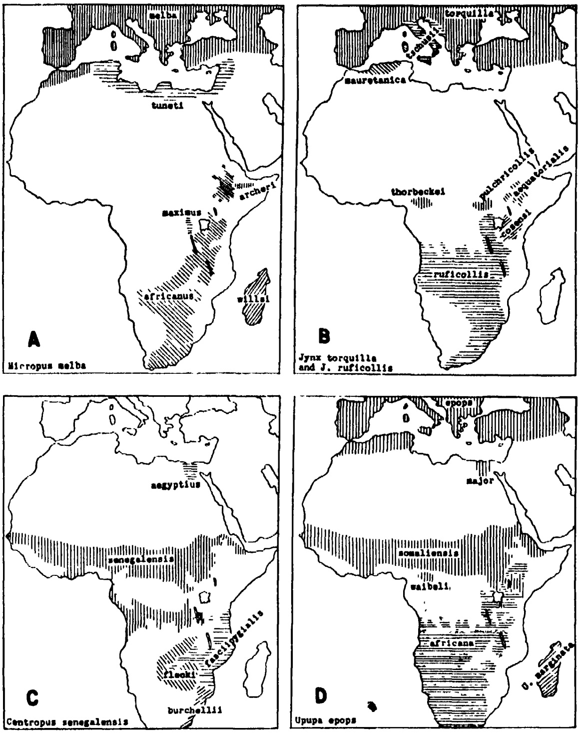

FIG. 7. Zonal distribution and the relation between the Palaearctic and Ethiopian Regions. *A, Micropus melba,* the White-bellied Swift, common to the Palaearctic and the Ethiopian Subtropical Zone; *B, Jynx torquilla,* the European Wryneck, and its African representative *J. ruficollis,* which is mainly a bird of the Ethiopian Subtropical Zone; *C, Centropus senegalensis,* a coucal occurring mainly in the Ethiopian Tropical Zone, but with a race, *flecki,* in a small part of the Subtropical Zone and another, *aegyptius,* in a small part of the Palaearctic Region; *D, Upupa epops,* the Hoopoe, a bird common to the Palaearctic and both the Ethiopian Tropical and Subtropical Zone (vertical shading forms with a white wing-bar). *U. marginata* is an allied species in Madagascar.

A similar relation between the southern Palaearctic and the Ethiopian Subtropical Zone appears to exist in the vegetable kingdom (Chipp, '30).

families, has been ascertained by a general analysis of the Ethiopian avifauna, and the limitation of examples to the latter is not to be interpreted, therefore, as indicating that the non-passerine families are in any way more subject to the influences of temperature than are the passerine families. The reverse is, if anything, more likely to be the case since most of the wide-ranging genera and species are to be found among the non-passeres.

Probably, as our knowledge of the Ethiopian fauna and flora increases, more examples of this type will be discovered in various groups of animals and plants. No attempt has been made here to account for the origin of this relationship between the avifaunas of the two regions. In our present state of knowledge, any explanations of this sort would be purely speculative. The above-listed examples are intended merely to indicate that a relationship does exist, and that temperature conditions are such that a slight interchange of avifaunas has occurred.

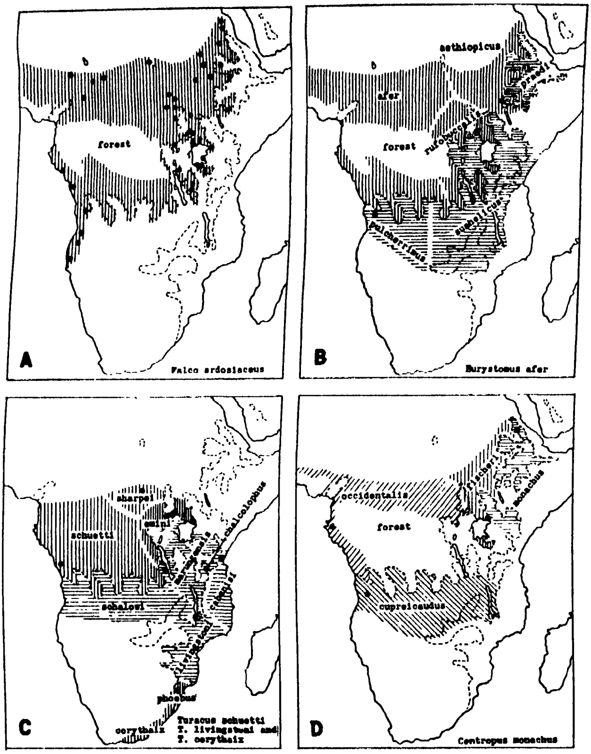

Fig. 8. The West African Province of the Tropical Zone as a center of avian dispersal. *A, Falco ardosiaceus,* the Gray Kestrel of the West African and Sudanese Province savannas (locality records black dots); *B, Eurystomus afer,* the Broad-billed Roller, of woodland and light forest invading neighboring parts of the Subtropical Zone (vertical shading forms with brown central upper tail-coverts, horizontal shading those with uniform blue upper tail-coverts, black dots type localities); *C, Turacus schuetti,* a Lourie of the West African Province forests, *T. livingstoni,* a species of the adjacent forest patches of the Subtropical Zone and the East Coast Province, and *T. corythaix,* a species of the Transition Zone in southeastern Africa (vertical shading forms with rounded crests, horizontal shading those with pointed crests, black dots type localities); *D, Centropus monachus,* a coucal illustrating a stage in the invasion of the Subtropical Zone from the West African Province (black dots type localities).

In a few cases, conditions the reverse of those outlined above, occur.

There are some birds common to both regions that suggest a closer relation of the Tropical, than of the Subtropical Zone of the Ethiopian Region, to the southern Palaearctic. The Hoopoe (*Upupa epops,* fig. 7, map *D*) is an example. Here the Subtropical Zone race, *africana,* differs markedly from the Tropical Zone forms, *somaliensis* and *waibeli,* as well as from the Palaearctic forms, *epops* and *major,* in lacking the white wing-bar.[10]

Possibly, through the distribution of another bird, a clue to this apparently reversed state of affairs may be found. The Senegal Coucal (*Centropus senegalensis,* fig. 7, map *C*) is distributed through the savannas of the Tropical Zone. In the upper Zambesi Valley the species has invaded a limited portion of the Subtropical Zone (race *flecki*). Likewise, at some time or other, it has invaded the southern Palaearctic Region, by way of the Nile Valley, and we have today a representative in Egypt, *aegyptius,* which has been completely isolated by arid encroachments in the middle reaches of the Nile. Possibly a similar explanation may be found for *Upupa epops;* the only difference here, apart from the more extensive invasions of the Subtropical Zone and the Palaearctic Region, being that a change in color pattern has accompanied the invasion of the Subtropical Zone, while no marked change has occurred during the invasion of the Palaearctic Region.

THE REACTION OF WIDE-RANGING SPECIES TO TEMPERATURE ZONES

Although the distributional limits of many species of African birds conform remarkably to the limits of a particular zone, there is a number of species whose occurrence in both the Tropical and Subtropical Zones calls for special remark. In a rough analysis (Bowen, '32) it has been estimated that, out of some 1,500 species (excluding high mountain forms, and certain families of marine and fresh water habitat) representative of the Ethiopian avifauna, about 1,150 occur wholly within the limits of a single zone. Of the remainder, about 100 seem to range indiscriminately through both the Tropical and Subtropical Zones, and about 250 exhibit subspecific differences coincident with the change from one zone to the other. It is to these 250 species that we will now turn our attention.

The geographical or subspecific variation of these is often so closely associated with zonal differences within their ranges that one is sometimes tempted to regard the relationship as one of cause and effect. It seems not unlikely, however, that in some cases at least, the physiological readjustment which undoubtedly accompanies the invasion of a new habitat or temperature zone, will stimulate the inherent tendency of a species to vary. A change in external form, coinciding with a change of environment, will result, but the one will not necessarily be the cause of the other. Instances of parallel varia-

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[10] The Subtropical Zone form, *africana,* is usually treated as a distinct species, thus limiting the range of *U. epops* to the southern Palaearctic, and the Tropical Zone of the Ethiopian Region. Recent material examined indicates, however, that *somaliensis* and *africana* intergrade, and the latter must, therefore, be treated as a subspecies of *epops.*

tion between two species invading the same ecological zone need not, therefore, be sought, since according to this view, the original impetus to vary is a genetic one, which is stimulated but not activated by the environment. The influences of isolation and natural selection as modifying agents directing the course of evolution cannot be doubted: environment can play both these rôles. It is not intended to enter here, however, into a discussion of the probable origin of subspecific change in relation to zonal distribution, but rather, by a study of the distribution of the avifauna as it exists today, to endeavor to trace successive stages, and in this way, to throw some light upon the subject.

The Tropical Zone as a Center of Avian Dispersal

Probably in no two species is the center of dispersal exactly the same. We may assume, however, that in the early stages of expansion of the range of a species, invasion of another zone is unlikely to occur until after all suitable territory within the zone of origin has been occupied. We may, therefore, select to start with a species whose distribution coincides with the limits of the zone, and then, by choice of others whose ranges have spread beyond these limits, endeavor to trace, stage by stage, the response of each species to the changed environment.

Because of the differences in temperature and rainfall and the manner in which the vegetation of the Tropical Zone is developed in belts of wide extent, it is not easy to find examples of species whose ranges extend through the entire zone. Usually the species of this zone occupy only one or other of the several characteristic vegetation belts. The bustards of the genus *Lissotis,* as we have already seen, occupy the savannas of this zone, and the doves of the genus *Calopelia* occupy the dense rain-forests: together they fill almost the entire zone. The White-collared Pratincole (*Galachrysia nuchalis,* fig. 6, map *C*) is an aquatic species, found on the rivers of this zone, both within and without the forests. It is absent from the East Coast Province, possibly because of the barrier formed by the highlands of East Africa, although it has reached the Zambesi Valley, evidently by way of the low country about Lakes Mweru and Bangweolo. The Green Coucal (*Ceuthmochares aereus,* fig. 6, map *D*), another forest bird, prefers light forest, second growth, and outlying gallery-forests, and so is found in the East Coast Province where the absence of heavy virgin forest precludes the existence of some forest forms such as the dove *Calopelia.*

The Gray Kestrel (*Falco ardosiaceus,* fig. 8, map *A*), a savanna species, is another instance of the many Tropical Zone birds to whose distribution the East African highlands have formed a barrier. The Broad-billed Roller (*Eurystomus afer,* fig. 8, map *B*), a bird of light forest and wooded savannas, has a distribution in the Tropical Zone similar to that of the Gray Kestrel, but unlike the latter, it has invaded adjacent portions of the Subtropical Zone and so has reached the East African coast. Of particular interest here is the fact that the three Subtropical Zone forms (*pulcherrimus, suahelicus,* and *praedi*) agree with one another in the possession of blue central upper tail-coverts, whereas the three Tropical Zone races have these feathers brown.

A somewhat similar, though more advanced stage, is found in a group of Louries of the forest genus *Turacus.* Here, the Subtropical Zone forms (*schalowi, marungensis,* and *chalcolophus*) differ specifically from those of the West African Province of the Tropical Zone, but are closely related to those of the East Coast Province (*livingstoni* and *cabanisi*). The latter form a link, in many respects, between the Subtropical Zone *schalowi*-group and the Transition Zone forms (*corythaix* and *phoebus*) which occur in the coastal regions of South Africa.

The distributional center of origin of the Coucal, *Centropus monachus,* and the apparent phylogenetic relationships of its races have been discussed by Friedmann ('30) who concludes that the dark-backed green-tailed form, *occidentalis,* represents, apparently, the original condition which has given rise, on the one hand to *cupreicaudus,* and on the other to *fischeri* and *monachus.* The relations of these four races to the life zones is shown in fig. 8, map *D.* It may be noticed that, whereas *cupreicaudus* and *monachus* are inhabitants of the Subtropical Zone, *fischeri* is a Tropical Zone form which owes its distinction from *occidentalis,* probably, to the isolating effect of the Nile-Congo divide.

The drier savannas and arid scrub-lands of the Sudanese Province of the Tropical Zone possess an avifauna characterized by an abundance of desert and semi-desert forms. Attention has already been called to differences in the avifauna of this arid belt due to differences in temperature in certain parts of it. Many species, however, range unchanged through its entire length. The Long-tailed Parrakeet (*Psittacula krameri,* fig. 9, map *A*) extends from Senegal to the Nile unchanged, yet in the somewhat cooler foothills of Abyssinia and Eritrea a slightly different form, *parvirostris,* occurs. The Black-head Plover (*Sarciophorus tectus,* fig. 9, map *B*), a dryland species of the Sudanese Province, has reached the North Kenya District of the Somalian Province by way of the low country around Lake Rudolf. The birds of the two provinces exhibit well-marked subspecific differences attributable, probably, to differences in temperature (fig. 4, map *C*) since the annual rainfall of the two provinces (fig. 2, map *B*) is approximately the same.

The Chestnut-bellied Sandgrouse (*Pterocles exustus,* fig. 9, map *C*), a bird of arid habitat, reaches the East African coastlands by way of the dry Somali coast. The form of the Somalian Province, *somalicus,* differs only slightly from the nominate form of the Sudanese Province, but in the Kilimanjaro and Loita districts of Kenya Colony, where the species invades the lower limits of the Subtropical Zone, a well marked race, *olivascens,* is found. A final stage, illustrating the invasion of the Subtropical Zone by a species characteristic of the dry Sudanese Province of the Tropical Zone, may be cited in the distribution of the Little Bee-eater (*Melittophagus pusillus,* fig. 9, map *D*). Here an almost complete invasion has occurred and indeed, in this and other similar examples, it is no easy matter to decide which of the two zones is the original and which the one invaded.

The East Coast Province owes its distinction from the remainder of the Tropical Zone chiefly to isolation for, although there is direct continuity by way of Somaliland and Abyssinia as well as by way of the gap between the Abyssinian and East African highlands, the connection with the rest of the zone lies through country entirely too arid for the requirements of many species. This province possesses a number of species peculiar to it: the Brown-headed Parrot (*Poicephalus cryptoxanthus,* fig. 10, map *A*) may be taken as an example. The Long-toed Lapwing (*Hemiparra crassirostris,* fig. 10, map *B*), has a similar distribution, although it has spread by way of the lowlying river valleys and lake shores and the Transition Zone areas of central Tanganyika Territory to adjacent parts of the West African Province.

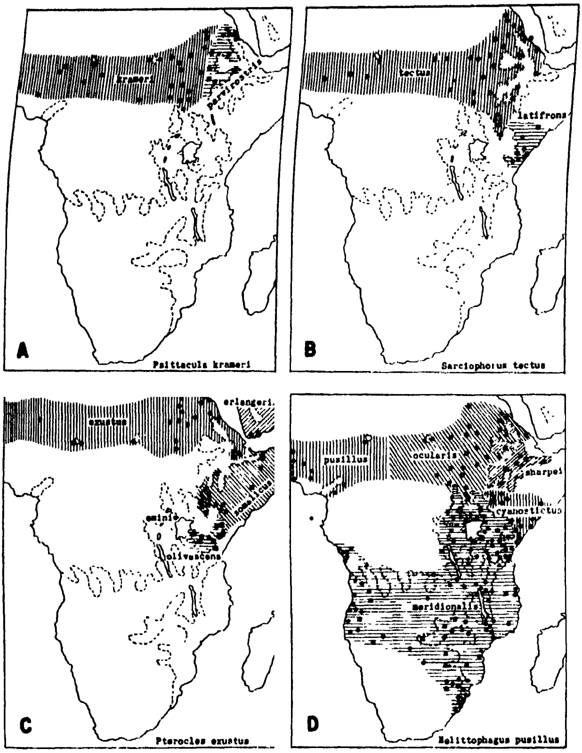

FIG. 9. The Sudanese Province of the Tropical Zone as a center of avian dispersal. *A*, *Psittacula krameri*, a parakeet of this province with a race, *parvirostris*, in the Abyssinian foothills; *B*, *Sarciophorus tectus*, a dryland plover with a distinct race in a part of the Somalian Province; *C*, *Pterocles exustus*, a sandgrouse of the Sudanese and Somalian Provinces invading a limited part of the Subtropical Zone (races *olivascens* and *emini*); *D*, *Melittophagus pusillus*, the Little Bee-eater, a species which has invaded a large part of the Subtropical Zone. Black dots indicate recorded localities.

The Brown-hooded Kingfisher (*Halcyon albiventris*, fig. 10, map *C*) presents a more advanced stage of an extension in this direction. Here, however, the species also has invaded portions of the Subtropical Zone (*viz.: H. a. albiventris* in eastern South Africa and *H. a. prentissgrayi* in the forests of Mt. Kenya). The Bare-throated Francolin (*Pternistis afer*, fig. 10, map *D*) has a similar, though more extensive, distribution. Here an invasion of the Subtropical Zone has occurred in several places (*viz.: P. a. itigi* in central Tanganyika Territory, *P. a. benguellensis* and *P. a. punctulata* in the Angolian Highlands, and the forms *swainsoni* and *damarensis*[11] in the interior of southern Africa.

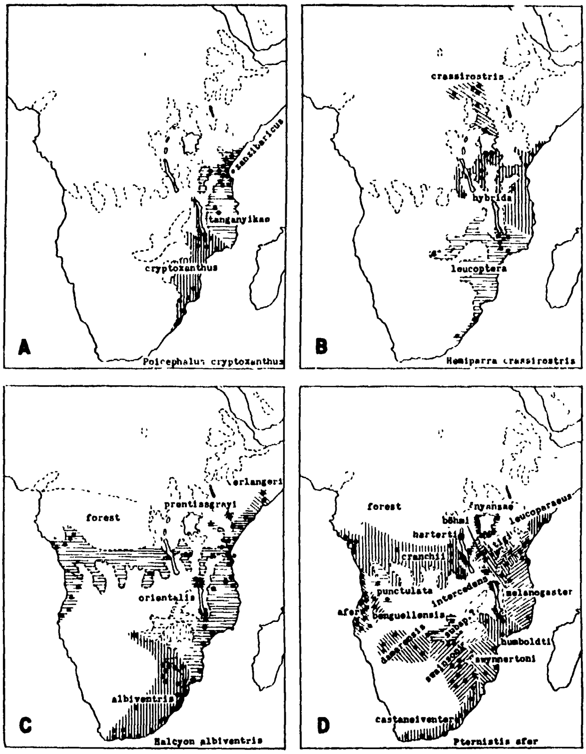

FIG. 10. The East Coast Province of the Tropical Zone as a center of avian dispersal. *A, Poicephalus cryptoxanthus*, a parrot of this Province; *B, Hemiparra crassirostris*, the Long-toed Lapwing, which has spread to parts of the West African Province by way of the low country in central Tanganyika Territory; *C, Halcyon albiventris*, a dryland kingfisher of the East Coast Province occurring also in the South Congo District and also with two races, *albiventris* and *prentissgrayi*, invading the Subtropical Zone; *D, Pternistis afer*, a bare-throated francolin with many races correlated with differences in elevation in the several places where invasion of the Subtropical Zone has occurred. Black dots indicate recorded localities.

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[11] In fig. 10, map *D*, following a previous revision (Bowen, '30), *swainsoni* and *damarensis* are made races of *P. afer*. However, a form of *swainsoni* has been described

The Subtropical Zone as a Center of Avian Dispersal

Temperature conditions along the east coast of Africa are influenced by winds from the Indian Ocean to the extent that, although tropical, these coastlands present a climate sufficiently equable to allow the invasion of many Subtropical Zone species which otherwise do not extend to the Tropical Zone.

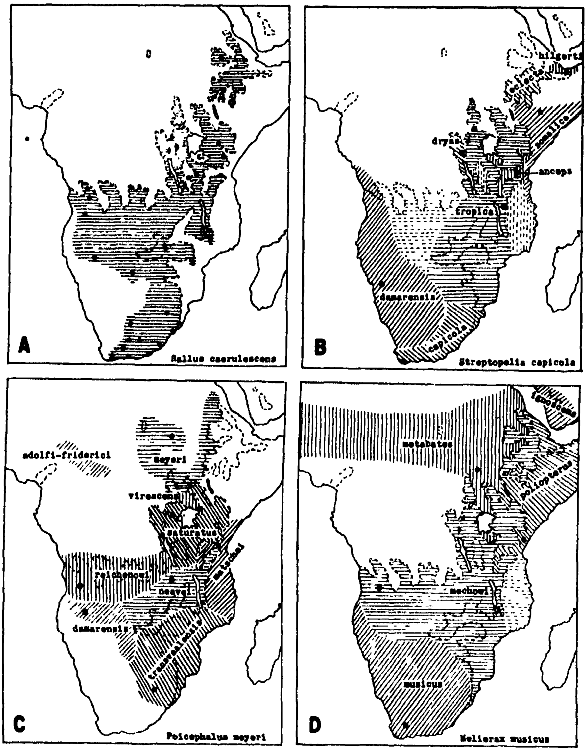

Fig. 11. The Subtropical Zone as a center of avian dispersal.

Distribution of: *A*, *Rallus caerulescens*, a rail characteristic of the Subtropical Zone (black dots indicate locality records); *B*, *Streptopelia capicola*, a dove of the Subtropical Zone invading the East Coast Province of the Tropical Zone; *C*, *Poicephalus meyeri*, a parrot of the Subtropical Zone invading the East Coast Province and a part of the Sudanese Province of the Tropical Zone; *D*, *Melierax musicus*, a Goshawk distributed throughout the Subtropical Zone, and invading the drier parts of the Tropical Zone. Black dots in *B*, *C*, and *D* indicate type localities.

Several examples of birds confined in their distribution to the Subtropical Zone have already been given: the Kaffir Rail (*Rallus caerulescens*, fig. 11, map *A*) is another. As an example illustrating the invasion of the East Coast Province, the Ring-neck Dove (*Streptopelia capicola*, fig. 11, map *B*) may be

recently from southern Angola, where *P. a. afer* is known to occur. *P. swainsoni* must, therefore, be given specific rank with *damarensis* and the newly described *gilli* Roberts as races.

selected because, although in several places uncertainty exists regarding subspecies, this dove presents several interesting points in its distribution. The five races, *capicola, damarensis, tropica, dryas,* and *eclecta,* occupy almost the entire Subtropical Zone, while *tropica* occurs also in the lowlands of the Zambesi Valley and southern Mozambique. The form *somalica* occurs in the southern part of the Somalian Province of the Tropical Zone, and extends south to the Pangani River. Another race, *anceps,* intermediate in character between *tropica* and *somalica,* occurs at intermediate elevations in Tanganyika Territory; its range will likely prove more extensive than is at present realized. The working out of the ranges of these three races, when adequate material is available, should be of value in defining the limits of the two zones in East Africa. Their altitudinal distribution is, according to Friedmann ('30), as follows: *S. c. somalica,* the coastal districts; *S. c. anceps,* below 5,000 feet but not in the coastal belt; *S. c. tropica,* above 5,000 feet.

The Brown Parrot (*Poicephalus meyeri,* fig. 11, map *C*) suggests, in its distribution, an initial stage of the invasion of the Sudanese Province of the Tropical Zone. The nominate form usually is stated as ranging from Eritrea through the Sudan to Kordofan, Darfur and the Bahr el Ghazal, but examination of locality records will show that only the more elevated parts of these countries are occupied. Comparison of the distribution map with a temperature map (fig. 1, map *A*) shows that this parrot does not occur in the hottest regions (*i.e.,* above 80° mean annual temperature). The Wryneck (*Jynx ruficollis,* fig. 7, map *B*), already cited as a Subtropical Zone species having a close relative in the Palaearctic Region, has a similar though not so extensive range. The Chanting Goshawk (*Melierax musicus,*[12] fig. 11, map *D*) illustrates a final stage in this series. Here we find a complete invasion of the more arid parts of the Tropical Zone.

SUMMARY

The concentration of forests in western equatorial Africa, as a result of the heavier precipitation there, and the consequent segregation of the majority of forest-inhabiting birds, has led to the recognition of a " West African Subregion," and to a somewhat exaggerated view of the importance of rainfall as a distributional factor in the Ethiopian Region. Because of the absence of any well-defined mountain system, the influence of temperature on African bird distribution has been underestimated. Besides Alpine and Temperate Zones on the isolated mountain tops, an extensive Subtropical Zone is recognized. The mean annual isotherm of 70° F. serves roughly as the boundary

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[12] There has been some dispute over the relationships of the several forms of this hawk, due to the occurrence of two forms in East Africa. Recent material examined convinces me that the five forms are conspecific, and that *mechowi* extends to the East African and Abyssinian highlands. This, and other taxonomic points alluded to in the present paper, are discussed in my report on the A. Blayney Percival collection of East African birds (in manuscript).

between this and the Tropical Zone, but a Transition Zone of varying width, wherein an overlap of the avifaunas of the two occurs, is recognized. A temperature map, made by combining isothermal maps of the mean minimum of the coolest month and the mean maximum of the hottest month, shows that both these zones are divisible into areas having wide seasonal ranges of temperature and areas of more equable temperature conditions. The former areas coincide with the regions of least rainfall. Ecological maps based on temperature, rainfall, character of vegetation and the distribution of many species of birds, and a classification of the region into life zones, climates, provinces and districts are provided.

The avifaunal relation between the Ethiopian Subtropical Zone and the Mediterranean parts of the Palaearctic Region indicates a similarity of climates. The majority of the species of the Ethiopian avifauna are distributed wholly within the bounds of the life zones delineated, but a few transgress these limits. In most of these latter cases, however, subspecific differences distinguish the inhabitants of each zone. A number of distribution maps are furnished to illustrate these points.

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NOTE

The first volume of Dr. Chapin's splendid work on the birds of the Belgian Congo (*Bull. Amer. Mus. N. H.*, **65**: 1–756, 1932), the first half of which deals largely with the distribution of bird life of the whole Ethiopian Region, was not read until after this paper was written. In this latest work, Dr. Chapin gives more credit to temperature as a distributional factor than he did in his paper of 1923. Differences in our respective viewpoints still exist, however, but space does not permit of their discussion here.

A TWENTY YEAR RECORD OF CHANGES IN AN ARIZONA PINE FOREST[1]

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In the early days of national forest administration one of the first thoughts of research men was to establish records that would make it possible to measure progress from time to time. Silviculture as applied to western conditions was largely theory; it was yet to be determined what methods would give the best results and whether, indeed, any method applicable under prevailing economic conditions would achieve the main object, namely, sustained production of timber under commercial utilization. So-called sample plots were established on logged over areas in order to ascertain how fast residual stands would grow, whether they could produce merchantable timber, and whether natural restocking would take place.

In the Southwest the first sample plots were established in 1909 by the Fort Valley Forest Experiment Station, now a branch of the Southwestern Forest and Range Experiment Station. The idea was conceived by Col. T. S. Woolsey, then chief of the Office of Silviculture in the Southwestern District of the U. S. Forest Service. The methods employed have been described elsewhere (Woolsey, '12). In brief, the areas vary in size from 2 acres on "intensive" plots to as high as 480 acres on "extensive" plots; all the trees were measured in diameter and about 10 per cent were measured in height. At first individual tree records were kept only on the relatively small intensive plots, but later all trees were numbered and recorded separately. Intensive plots were also mapped in detail, locating all tree groups, all seedlings and saplings, stumps, logs, brush piles, logging roads, and other features which might affect growth and reproduction (figs. 1 and 2). Between 1909 and 1915, there were established in the ponderosa pine[2] forests of Arizona and New Mexico 7 extensive plots, having a combined area of 1315 acres, and 50 intensive plots having a combined area of 222 acres. All plots have been examined and remeasured at 5-year intervals, the longest records now covering a span of 20 years.

The present paper deals with a plot of 480 acres established in 1909, on the Tusayan National Forest in northern Arizona. Two subdivisions of 12 acres each within the larger plot are designated as intensive plots.

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[1] The publication of extra illustrations with this article was made possible by funds other than those of the Ecological Society of America.

[2] The name "ponderosa pine" has recently been adopted by the U. S. Forest Service in place of "western yellow pine" as the official common name of *Pinus ponderosa*.

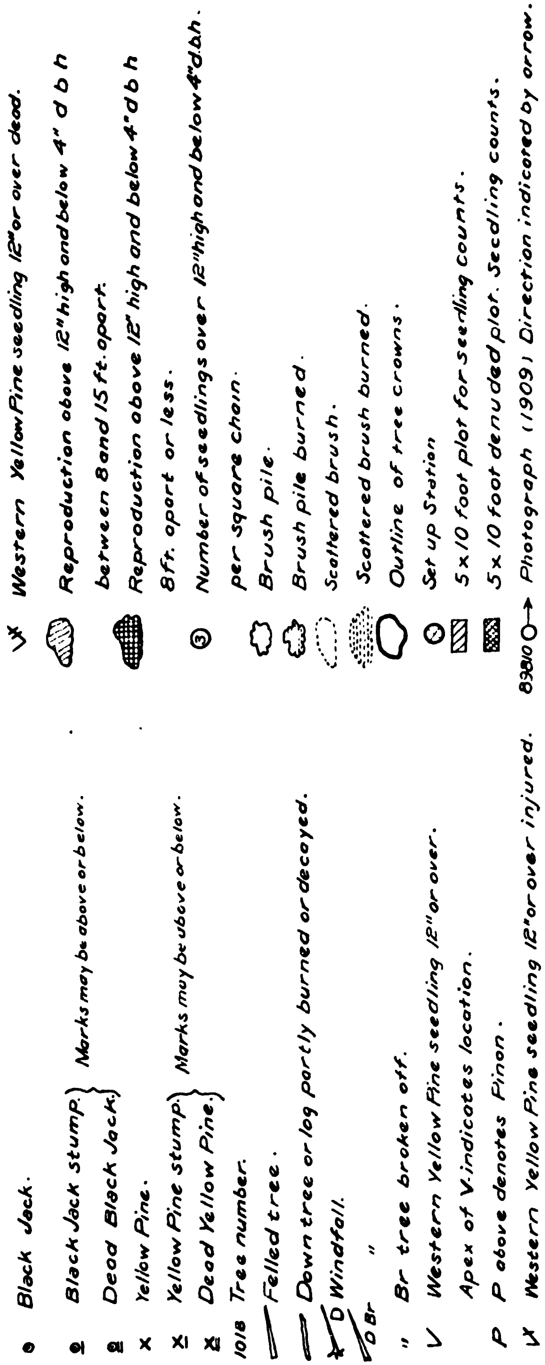

FIG. 1. Legend used in mapping sample plots shown in figures 2 and 6.

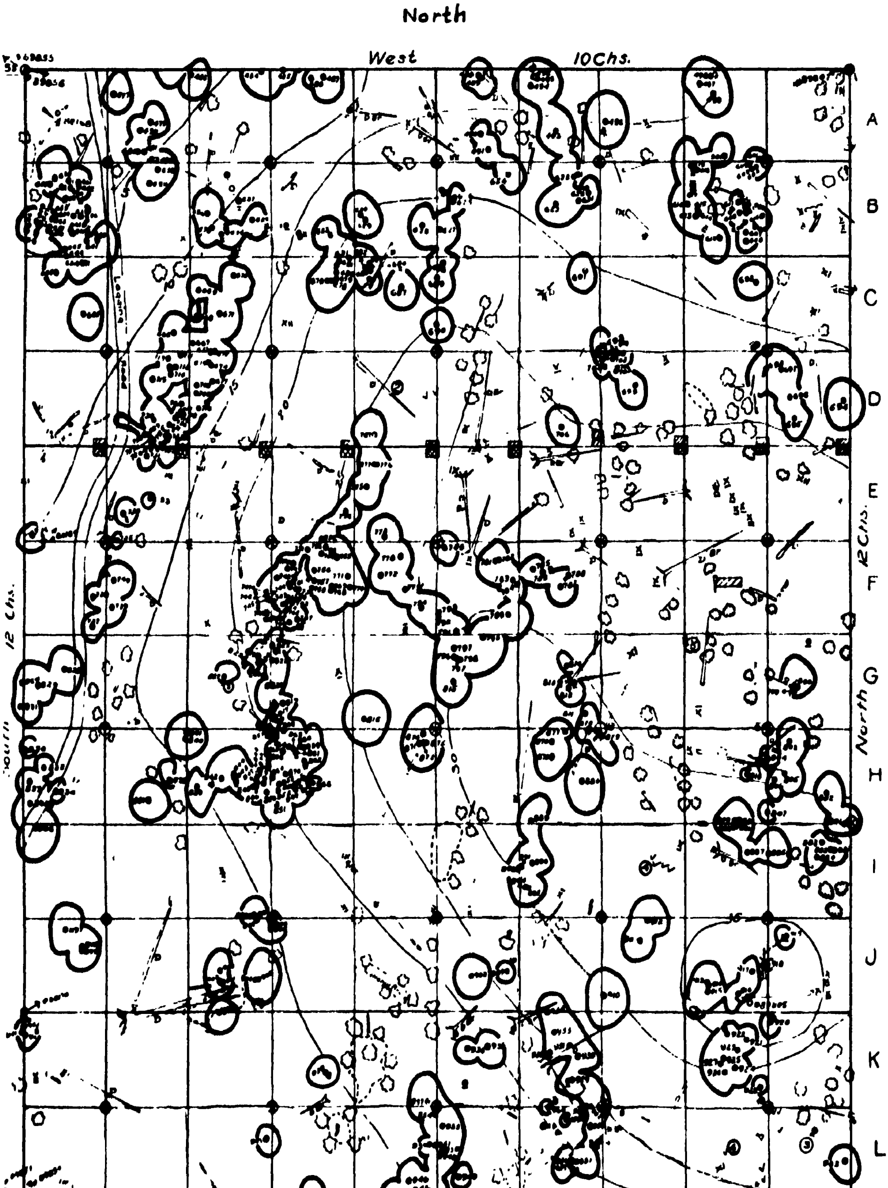

FIG. 2. Sample plot S 3-B, Tusayan National Forest, established in fall 1909, logged summer 1909. Contour interval 5 ft., scale: 1 in. = 1 chain. Mapped by E. W. Nelson, October, 1914.

The forest before cutting was typical of the pine forests of the Colorado Plateau. A marked characteristic of these stands is that the trees occur in more or less even-aged groups separated by open spaces, often larger than the groups themselves. An exact record of the original volume is not available but it is estimated to have been about 9000 feet B. M. per acre. Cutting took place in 1909, under what is known as the group selection method, deriving its name from the practice of treating the group as a unit, cutting or leaving according to the age or condition of the group. Mature groups (yellow pine) were cut clear except that selected individuals were occasionally left where needed for seed; groups of immature trees (blackjack) and middle aged trees (intermediate) were left subject to thinning and removal of diseased and defective individuals. Seedlings and saplings below 20 years of age were almost entirely absent and the number below 60 years was relatively small. A dense growth of bunch grass, *Festuca arizonica,* occupied the open spaces which under normal conditions should have been stocked with young pine. The general character of the forest after cutting is shown in figures 3*A* and 4*A*.

The climate, topography and soil of this plot are typical of a large section of the pine forest in northern Arizona. The altitude is about 7300 feet; annual precipitation is between 22 and 23 inches, about 45 per cent of which comes in winter, mainly in the form of snow, and most of the remainder in summer rains during July, August and September. The mean annual temperature at a station of the same altitude 5 miles to the east is 45.6° F. and during the growing season, June 1 to September 30, it is 61° F. The mean maximum and mean minimum temperatures for the growing season are 77° and 45°, respectively. The topography is gently rolling. The soil is derived from basalt and varies from a clay loam to a loamy clay. It is mixed with varying proportions of gravel and stone. Soil moisture is abundant during the spring months up to June first when it begins to decline, approaching wilting coefficient in the upper foot by the end of June. In July it rises again as a result of the summer rains and usually maintains an available margin of from 5 to 10 per cent until the middle of October when it is likely to decline again nearly to the wilting point. Pine seedlings usually germinate during July rather than in the spring because during the spring period when moisture is adequate the temperature is too low for germination, and after the temperature becomes favorable the soil is too dry in the upper layers.

What the Records Show

The periodic examinations have shown consistent growth of trees in diameter, height and volume, considerable mortality throughout the period, and irregular though ultimately effective reproduction.

Number and Sizes of Trees. The cutting left an average of 18.1 trees per acre, counting only those 4 inches and over in diameter, measured at a point 4.5 feet above the ground. Comparison with areas on which natural restocking has proceeded normally over a long period reveals a marked deficiency of trees in and below the 4–11 inch class. The number over 20 inches in diameter compares favorably with the best cutover areas in this region. Trees of this size are the most effective seed bearers and they also form a substantial nucleus for the next crop of timber to be cut after about 60 years.

Periodic re-grouping by diameter classes will show a gradual moving up from the lower to the higher classes as a result of diameter growth. Thus, many of the 4–11 inch trees will pass over into the 12–20 inch class and many of those in this class will in turn pass into the 21–30 inch class. In a stand where reproduction has proceeded normally there will usually be large numbers of young trees attaining the 4-inch diameter each year, and thus each 5-year measurement should record a substantial number of new trees in the 4–11 inch class. Because of the deficiency in seedlings when the plot was first measured, the 4–11 inch class has received few additions from below and it contains fewer trees now than in 1909. Moreover, the entrance of new trees above 4 inches in diameter has been more than offset by mortality and therefore the total number on the plot has declined since the first measurement.

TABLE I. *Increment and mortality in a ponderosa pine forest during twenty years after cutting. Sample plot* **S–3**, *area .456 acres, Tusayan National Forest, Arizona*

Unit of measure[1]	Volume per acre after cutting	Net annual increment per acre		Annual mortality per acre	
		Actual	Per cent	Actual	Per cent
Cubic feet	737	15.1	2.05	4.1	0.56
Board feet	3,520	91.0	2.59	20.0	0.57

[1] Cubic volume includes all trees 4 inches and over in diameter; board foot volume (Scribner Decimal C scale) includes only trees 12 inches and over.

Diameter Growth. Diameter growth of blackjacks or immature trees has proceeded at an average rate of 1.46 inches in 10 years. The older trees or yellow pines have grown at a somewhat slower rate but they are not included in table II because the total number on these plots is too small to give a representative average. Periodic measurements show some fluctuations and a slight decline in the last 5-year period. Whether this is the beginning of a downward trend remains to be determined. It is of interest to note that the 21–30 inch trees have grown slightly faster than the 4–11 inch trees and almost as fast as the 12–20 inch trees. The difference in rate of growth between diameter classes is so small that for practical purposes blackjacks of all sizes may be assumed to be adding to their diameters at the same average rate. All plots in this region show this relation. Since it requires much more wood to deposit a ring on the outside of a large trunk than a small one it would be logical to expect a decline in diameter accretion of the larger trees.

This probably will take place as the stands tend to become fully stocked. During the 20 years represented by these records, however, there evidently has been room enough for both crowns and roots to expand sufficiently to keep pace with the increasing size of the trunks.

TABLE II. *Diameter growth in relation to size of trees*[1]

Diameter class	Trees in each class	Mean annual diameter growth
Inches	Number	Inches
4–11	392	.142
12–20	434	.150
21–30	101	.146

[1] This tabulation is based on intensive plots only because individual trees on extensive plots were not tagged in the beginning of the study. Only blackjacks or trees below about 180 years of age are included because older trees on the intensive plots are too few in number to furnish a reliable average.

Volume Increment. Increase in volume per acre expresses the summation of the factors of growth and mortality. Cubic volume gives the most accurate measure of increment; board foot volume is the commercial unit of measure. The cubic volumes in table I include all trees down to 4 inches in diameter, but the board foot volumes include only those above 11 inches. Net increment, after deducting the volume lost by death of trees, has averaged 91 feet B. M. per acre annually. The volume left in cutting was 3520 board feet per acre, hence the average annual increment amounts to 2.59 per cent. If the past rate of growth continues for 60 years from the time of cutting the volume will have increased to 8980 board feet per acre and it will then be possible to make a second cut equal to the first, without reducing the original wood capital or growing stock. Whether this rate of increment will continue 60 years depends upon several factors. It is not likely that the gross volume production will fall off but an increasing rate of mortality may decrease net increment. On the other hand, it should be recognized that less than one-half of the land area is now occupied by trees beyond the sapling stage. The openings are about two-thirds stocked with seedlings nearly all germinated since the cutting, large numbers of which will pass the 11 inch mark at an age of 60 to 80 years. The increment as expressed in board foot measure may decline in the next 40 years, but the cubic increment is bound to increase, and this will eventually be reflected in board foot volume. Present indications are that after this area has been under management long enough to obtain full stocking and a balanced distribution of age classes, a sustained annual yield of 150 board feet can be realized.

Mortality. As has been indicated, growth is in a measure offset by mortality and as a stand approaches maturity, mortality may become a deciding factor in determining whether the volume of the stand increases, decreases, or remains stationary. Obviously, death results in the greatest loss when it takes large trees; small trees are for the most part quickly replaced by expanding neighbors, but when a veteran of 30 inches or more succumbs it not only removes a large volume of wood but it also leaves a gap which is not quickly filled. An analysis of mortality in relation to size of trees and factors responsible for their death on this and other plots has been presented by Krauch ('30). Krauch's study shows that the greatest number of large trees and hence the greatest volume is destroyed by windfall and lightning. Mistletoe has killed a larger number of trees on this plot than any other agency, but it is most active on young or middle-aged trees; its effects are felt even more in reducing the rate of growth than in the outright killing of trees.

Natural Reproduction. Natural reproduction is the most complex and ecologically the most interesting and important phase of forest management. In the preceding discussion it has been brought out that sustained volume production is dependent upon consistent restocking; attention has also been called to the absence of seedlings on this area at the time of cutting. The reproduction recorded in this study may, therefore, fairly be credited to silvicultural practice. This consists briefly of the following measures: (1) Leaving adequate seed trees (in this instance 4.4 selected trees per acre, having a diameter of over 20 inches, plus a large number of smaller trees); (2) Complete elimination of fire; (3). Regulation of grazing.

Detailed discussion of the factors affecting natural reproduction has been presented elsewhere (Pearson '23). In brief, successful restocking is dependent upon proper coincidence of seed crops and rains accompanied and followed by adequate protection against fire, grazing, and rodents; secondary factors are character of soil and herbaceous vegetation.

During the first 10 years of the study progress in reproduction was so slow that success was almost despaired of at the time (figs. 3*B* and 4*B*); subsequent experience has shown that the rate of progress was about normal for this region. This, however, applied only to the two intensive plots which were fenced against grazing animals; on the extensive plot exposed to severe grazing by cattle and sheep the only seedlings that became established were in partially protected situations, as among rocks and along logs with protruding branches. A survey of the intensive plots in 1918, nine years after cutting, showed that seedlings over 2 years old were present in numbers varying from 0 to 500 per acre on different sites. The contrast between overgrazed and protected plots here and on the other areas on the Colorado Plateau demonstrated that of the factors within the control of man grazing was the one which most needed attention.

In 1919, an extraordinary combination of seed and rainfall resulted in pine germination and survival unequalled in the history of national forests of the Southwest. Records of this seedling crop have confirmed and supplemented previous findings especially with reference to the influence of browsing

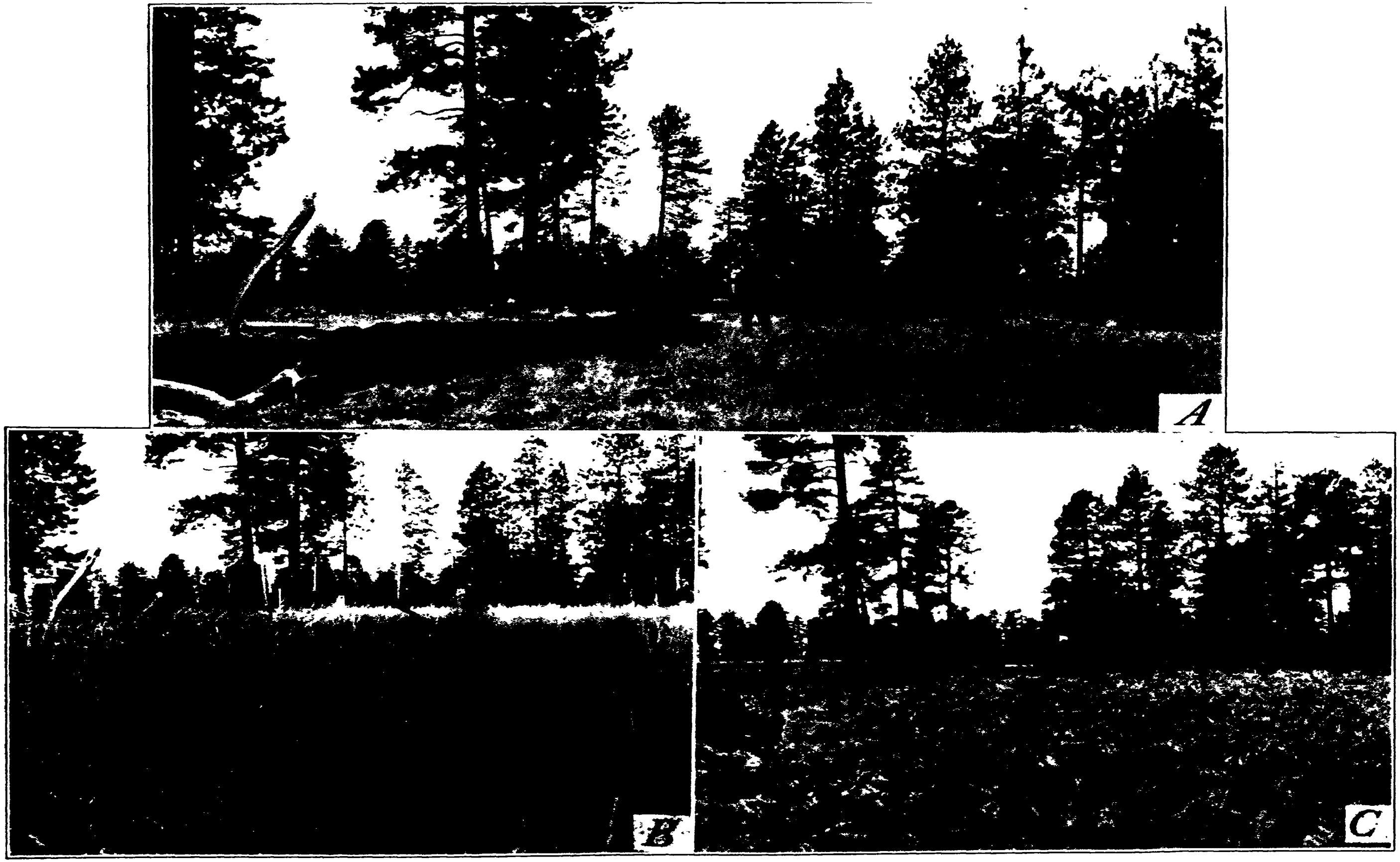

Fig. 3. Openings in ponderosa pine forest after logging. *A*. Immediately after logging in 1909, the ground occupied by Arizona fescue. *B*. Five years later; no grazing, grass very luxuriant, no reproduction. *C*. Twenty years after cutting, grass matted by preceding winter's snow: no reproduction in dense grass but good reproduction in background where grass is of only moderate

Fig. 4. Progress of reproduction after cutting. *A*. In 1909, immediately after cutting. *B*. Ten years later; a few seedlings present but hidden in the grass. *C*. Twenty years after cutting; the area for the most part well stocked with seedlings of 1914, 1917, and 1919 germination.

by livestock. Seedlings were killed on a large scale in 1919 and 1920, but they were so abundant on this area that survival remained adequate in most places. Substantial reduction in the number of grazing animals was made in 1921. Considerable damage continued but it was not severe enough to cause the death of many seedlings. In 1926, cattle were excluded and additional reductions were made in both numbers and length of grazing season for sheep. Since 1926, browsing has largely disappeared except on relatively small congested areas such as bed grounds. Recovery of seedlings damaged prior to 1926 has been phenomenal. A large per cent of those which had been browsed down to bush form have developed vigorous leaders. More severely injured specimens are still bushy but are clearly on the road to recovery (fig. 5*B*). Substantially the same remedial measures were applied with similar results on extensive areas adjoining the sample plots. Whether a range is grazed by sheep or cattle appears to be of secondary importance so long as the numbers are not excessive and they are kept properly distributed over the range.

Figures 2 and 6 present charts of the intensive plot S 3 B prepared in 1914 and 1931. The 1914 map is essentially a completed edition of the original one made in 1909. Except for natural reproduction the changes recorded in 1931 are not striking; occasionally a large isolated tree has dropped out or a break in the crown outline has resulted from the death of a tree in the edge of a group. No new crowns have entered the canopy. Careful measurement would show a small expansion in crown dimensions but the changes are too small to be recorded on this map. Stumps and logs have disintegrated considerably but they are still plainly evident. Logging roads have been obscured by vegetation in some places, in others they are as clearly outlined as 20 years ago.

The most evident change is in the natural reproduction. For the most part the spaces between tree groups are adequately stocked with young trees a great majority of which are of 1919 origin. A large per cent of the older seedlings present in 1918 were killed by porcupines, a pest which was controlled in time to avoid serious damage to the 1919 seedling crop. Notwithstanding the very prolific and well distributed germination in 1919, there are now patches of considerable size that are poorly stocked. Seedlings started in these places but they died, mainly in 1920. A soil map prepared in 1919 by J. O. Veatch, at that time a member of the Bureau of Soils, U. S. Department of Agriculture, shows that the poorly stocked areas usually have a relatively fine and compact soil described as clay loam or loamy clay. These sites also bear a very luxuriant growth of bunch grass, *Festuca arizonica*. The well stocked areas have a more gravelly or stony soil and a light or moderate stand of mountain muhlenbergia, *Muhlenbergia montana*, also a bunch of grass, usually less aggressive than the *Festuca*. Counts in 1920 on several 1/10 acre plots gave for the heaviest soils only 36 of the older seedlings per acre as against 493 for the stony soils. Whether the adverse influ-

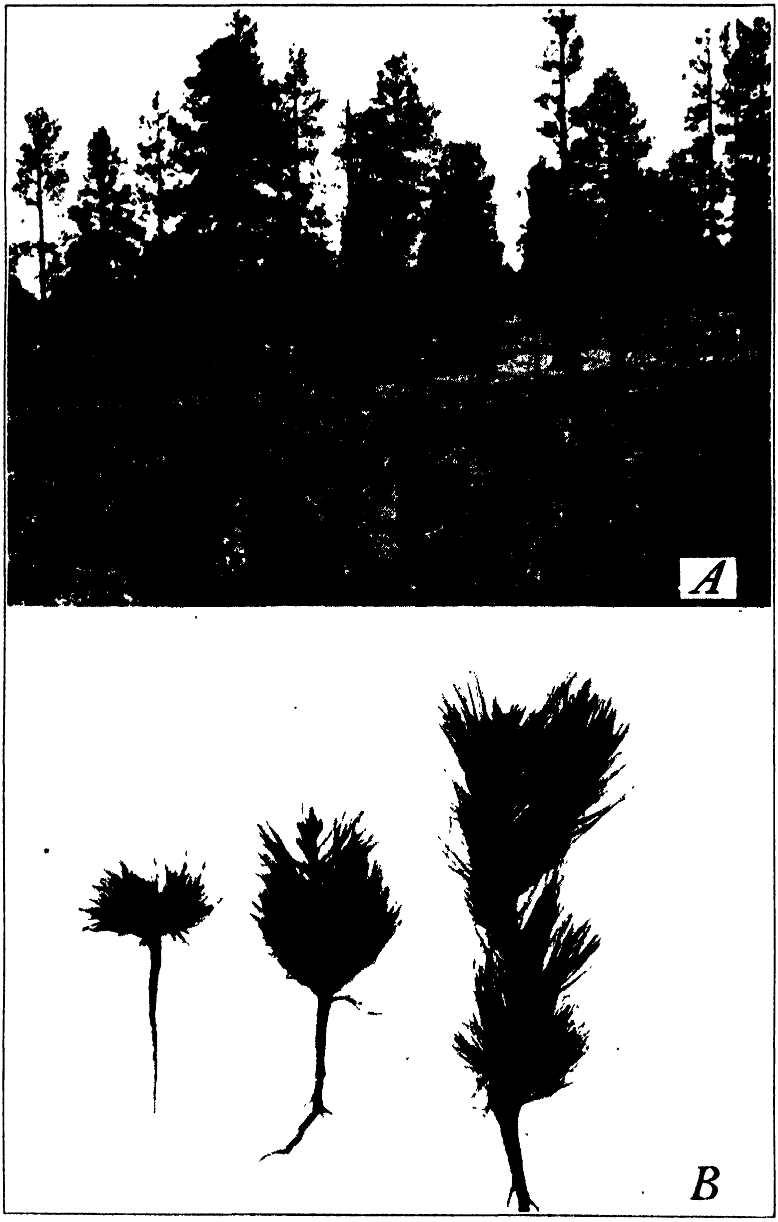

Fig. 5. *A.* Excellent reproduction well distributed; all has originated after cutting. *B.* Progressive stages in the recovery of pine seedlings injured by grazing shown from left to right. During the first year or two after damage ceases a dense growth of leaves develops; a leader is then formed and growth becomes rapid. Note the dense foliage and sharp bend at the base of the large specimen, indicating point of injury.

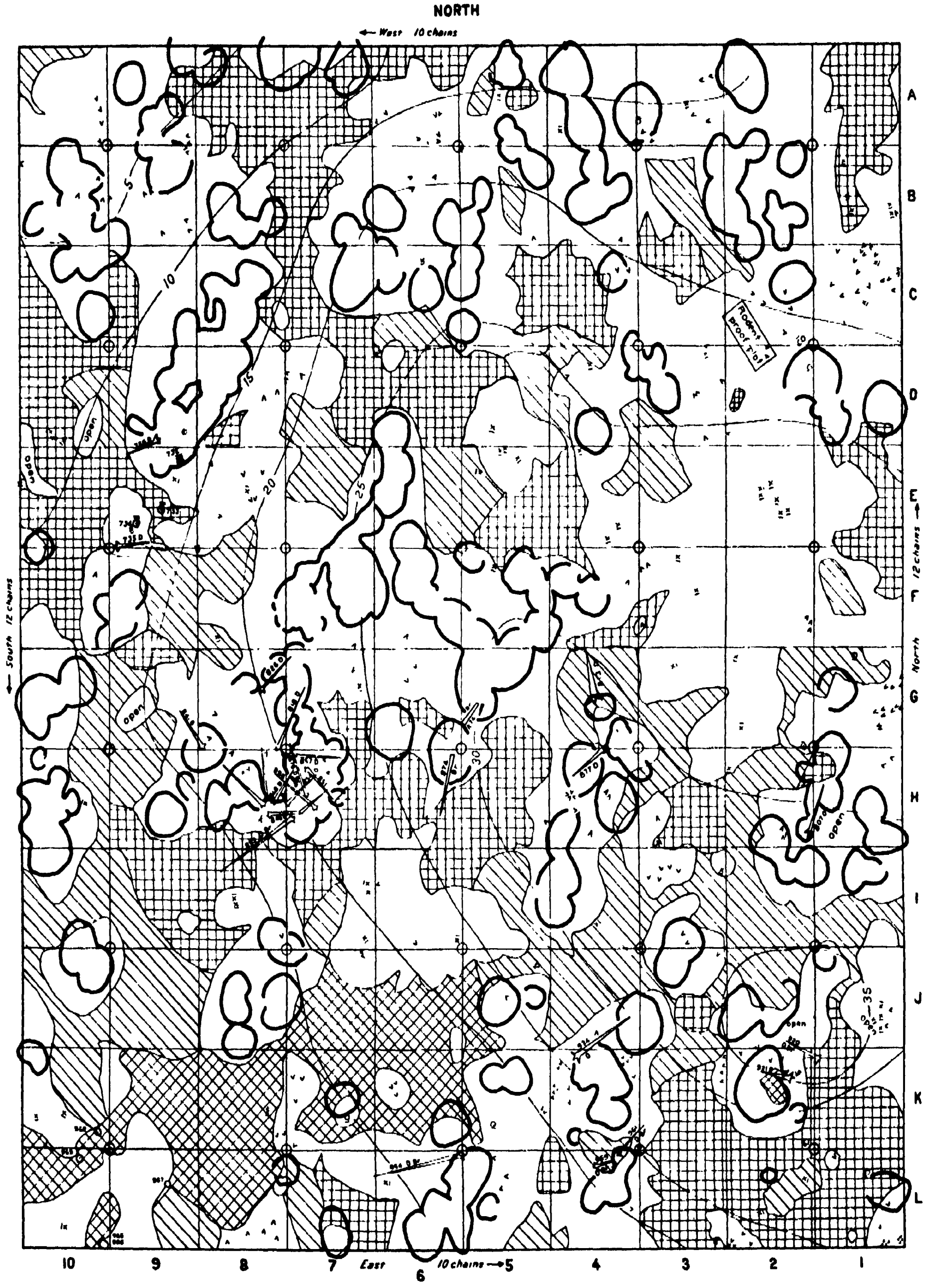

FIG. 6. Same plot as shown in figure 2, seventeen years later. Mapped by E. M. Hornibrook, June, 1931.

ence on the poorly stocked sites was due mainly to the finer soil or to the greater grass competition is still somewhat of an open question. Where the heavy soils are cleared of grass without destroying the surface leaf mold, usually present in undisturbed stands of bunch grass, pine seedlings readily become established and make a vigorous growth; on the other hand, where the grass is killed out by trampling or deep cultivation, exposing the clay soil, the seedlings almost invariably die. It is undoubtedly true that the clay soils are unfavorable to pine seedlings in early life unless organic matter is incorporated in the upper layers, or unless the soil is covered by some sort of mulch such as dead grass, needle litter, or limb wood. It is also true that a luxuriant stand of grass or other vegetation which has prior possession of the soil subjects a young seedling to competition for moisture and light that is likely to prove fatal. Since the heavy soils support the heaviest growth of grass they impose a double handicap on the pine seedlings, whereas the light soils, usually bearing a relatively light stand of grass, are doubly favorable.

It is a curious anomaly that the stony soils which restock most readily often produce the poorest timber and conversely the finer soils which restock with difficulty produce the best timber if an adequately dense stand of trees once becomes established. It is, therefore, important for the forester to see to it that reproduction does not fail on these most productive sites. Artificial removal of the grass, leaving the surface mold, would undoubtedly bring results, but at high cost.

Grazing, regulated in such a manner as to hold the grass in check, at the same time avoiding prolonged over-grazing and the attendant soil deterioration, promises to be a favorable middle course. This idea is supported by the fact that although the ungrazed plots in this experiment had a great advantage in early protection, the grazed plot today is more uniformly stocked, there being fewer and smaller areas on which the grass was able completely to suppress the tree seedlings in their infancy.

SUMMARY

An area of 480 acres of ponderosa pine logged in 1909 was divided into three plots, one extensive plot of 456 acres, and two intensive plots of 12 acres each. Cutting followed the general practice in the national forests in which about one-third of the merchantable volume is left, mainly in the form of immature trees. All trees over 4 inches in diameter have been measured at intervals of five years. The intensive plots were mapped in 1909, 1914 and 1931, showing the location of all trees and groups of seedlings, in addition to other features.

According to the 1909 record there were on the extensive plot after cutting 8248 trees over 4 inches in diameter, or 18.1 per acre. During the 20 years up to 1929, 847 of these trees died, representing an annual loss of 20 board feet per acre. The agents listed as responsible for this mortality are mistletoe, wind, lightning, bark-beetle and suppression. The net annual increment per acre, after deducting the above loss, is 91 board feet or 2.59 per cent of the 1909 volume. This rate of growth would permit in 60 years a second cut equal to the first, without reducing the growing stock.

On the extensive plot natural reproduction was a total failure up to 1919, because of over-grazing. During this time fairly good progress had been made on the intensive plots protected against all grazing. In 1921 and again in 1926, the number of livestock was reduced, with the result that grazing damage has greatly decreased, and natural reproduction is now proceeding satisfactorily.

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ADDITIONAL INFORMATION ON PRECIPITATION AS A FACTOR IN THE EMERGENCE OF *EPILACHNA CORRUPTA* MULS. FROM HIBERNATION

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Introduction

Questions repeatedly asked in relation to emergence of the Mexican bean beetle (*Epilachna corrupta* Muls.) from hibernation are, when does natural emergence start, how long is the period of emergence, and at what time of the season do overwintered beetles enter the fields? In an endeavor to answer these questions the study of the emergence of this insect from cage and natural hibernation, which was conducted from 1924 to 1926, inclusive, in the Estancia Valley, N. Mex. (Douglass, '28), has been continued and extended to include data secured in 1930, with some supporting experiments from the years 1927 to 1929.

Emergence from Cage Hibernation

Cages

The hibernation cages were constructed of 2 by 4 inch lumber and were 4 to 6 feet wide, 4 to 6 feet long, and 3 to 4 feet high. They were covered with 14-mesh screen wire and had removable tops. The tops were removed after the beetles had become dormant and were replaced before activity was manifested in the spring. In this manner conditions approximating, as nearly as possible, those prevailing in the surrounding areas were secured.

Six cages—Nos. 5 to 10, inclusive—were used in these studies. Cages 5 to 9 were all located in the western yellow pine (*Pinus ponderosa*) forest zone (fig. 1), which covers the higher rolling hills along the foot of the Manzano Mountains and the lower and drier slopes of the mountains. The cages are situated on different slope exposures and represent a typical cross section of the beetles' natural hibernation quarters. Cage No. 10 was located in the Piñon Cedar association that clothes the lower rolling foothills immediately below the western yellow pine consociations.

Material

The hibernation material consisted of a combination of oak leaves and pine needles, exceptions being cage No. 6, where pine needles alone, and cage No. 10, where piñon and cedar needles, were used.

Beetles used during the hibernation season of 1929–30 were collected from September 9 to 17, inclusive, in canyon and foothill fields of the Estancia Valley. During the fall of 1929, when field beetles were seeking hibernation, the numbers of beetles (table I) were placed in the cages:

FIG. 1. Western yellow pine that covers the higher rolling hills and the lower and drier slopes of the mountains. This is a view of the Tajique Canyon area where the cages were located.

Methods

During most of the season, the cages were examined daily. On days that observations were made, the active beetles (those on the screen) were removed from the cages, and the numbers thus removed were used in computing the percentages of the total number of beetles which emerged during the spring and summer.

The temperatures were taken from records obtained with thermographs which recorded both the temperature of the air and that of the hibernation material in cages near by. All the daily temperature averages, both for the cage and for the natural hibernation experiments, were computed from 12 readings per day taken at 2-hour intervals from the thermograph records. The precipitation data for the cage experiments are the mean rainfall records obtained from two gauges maintained in the Tajique Canyon, one near cage No. 5 and one near cage No. 8.

Observations

The first active beetles were noted on April 23. These beetles later reentered the hibernation material. They continued to appear and disappear at irregular intervals until May 20, when the removal of active beetles was

TABLE I. *Emergence from hibernation in cage Nos. 5 to 10, inclusive, during 1930*

Weekly period ending	Mean temperature			Precipitation	Beetles emerging from hibernation in cages						Total beetles emerged
		Hibernation material									
	Air	Cage No. 5	Cage No. 7		No. 5 7,050 feet	No. 6 7,050 feet	No. 7 7,000 feet	No. 8 6,975 feet	No. 9 6,980 feet	No. 10 6,800 feet	
	° F.	° F.	° F.	inches	Number	Number	Number	Number	Number	Number	Number
May 26	53.1	48.1	56.0	T.	2	3	9	1	67	0	82
June 2	52.9	49.2	56.3	0.55	5	7	24	3	114	0	153
9	57.0	52.1	60.9	0.00	16	7	29	0	99	0	151
16	61.6	55.8	65.0	0.08	42	20	50	0	286	1	399
23	64.6	57.2	66.2	T.	41	36	110	0	345	12	544
30	65.4	56.7	66.1	T.	130	48	130	3	293	12	616
July 7	65.2	54.6	65.7	0.38	887	193	514	122	1,505	4	3,225
14	61.7	56.0	63.6	1.52	493	263	270	144	1,212	3	2,385
21	61.2	56.2	63.4	2.09	36	48	39	51	407	0	581
28	59.1	55.9	62.3	2.57	2	2	0	3	17	0	24
Total emerged					1,654	627	1,175	327	4,345	32	8,160
Total beetles placed in cages					10,000	2,500	10,000	5,000	20,000	2,500	50,000

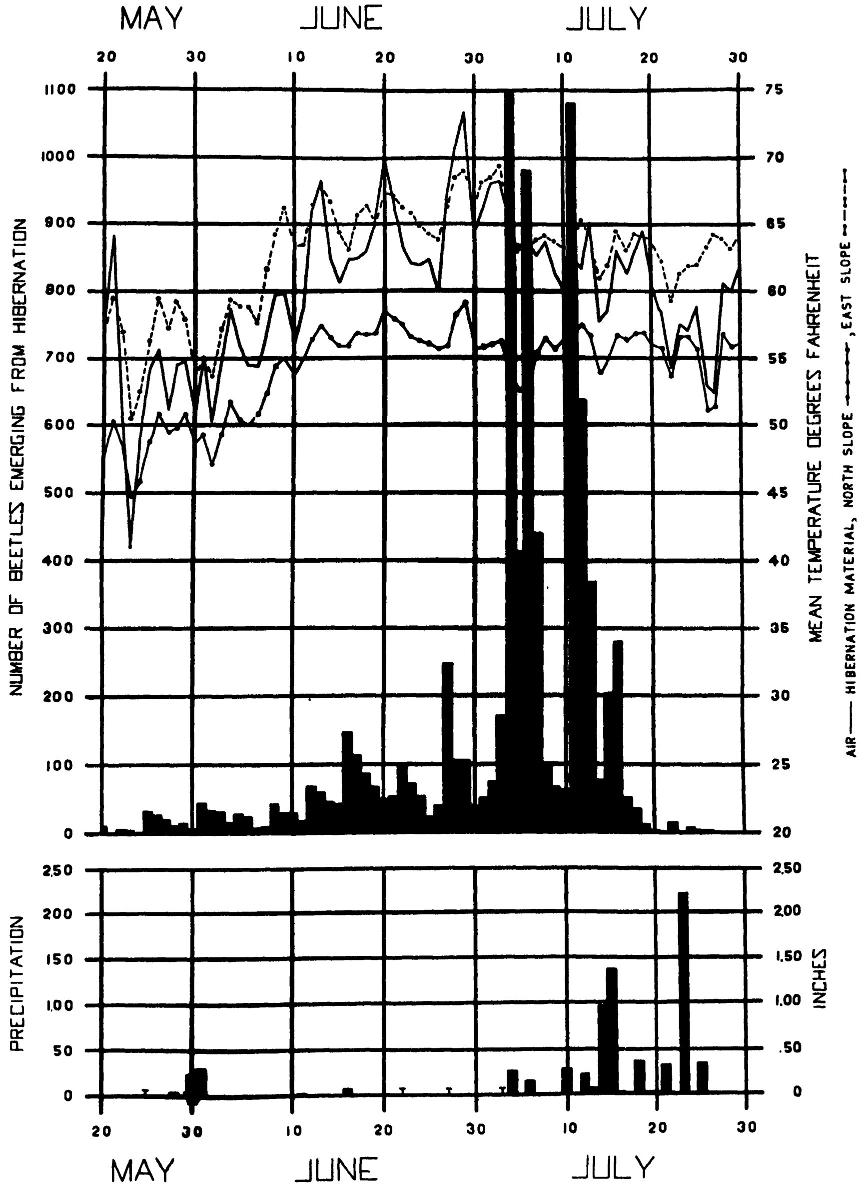

FIG. 2. Emergence of Mexican bean beetles from cages Nos. 5 to 10, inclusive, located in the foothills of the Estancia Valley, during the emergence season of 1930.

started. The first permanent emergence probably occurred May 31, when 32 beetles were noted on the screen of cage No. 9. Two pairs were observed mating in the same cage on June 1. This cage was situated on a warm southern exposure and the hibernation material was wet from recent rains. The last beetle emerged in the cages on July 27, 95 days after activity was observed. The period of emergence, exclusive of temporary activity, covered a period of 58 days, from May 31 to July 27, inclusive, with two distinct peaks of intense emergence, as shown in figure 2.

The first peak occurred on July 4 and the second on July 11. The greatest emergence took place from July 4 to 13, inclusive, when 5,244 out of 8,160, or 64.26 per cent, emerged. This period includes 3 days (July 8 to 10) in which only 224 beetles emerged, as shown in figure 3. On July 4, from about 11.30 A.M. to 12 noon, there was a local shower in the Tajique Canyon area in which the cages were located, but in a short time the sky cleared and the sunshine was intense. Numerous beetles were noted on the wing, flying up or down the canyon with the changing wind. At 11.30 A.M. the temperature was 84° F., at 12 noon it had fallen to 56° F., and by 2 P.M. it had risen to 80° F. It appeared that the contact moisture started the emergence, and that the rise in temperature following the rainfall acted as a stimulus for emergence.

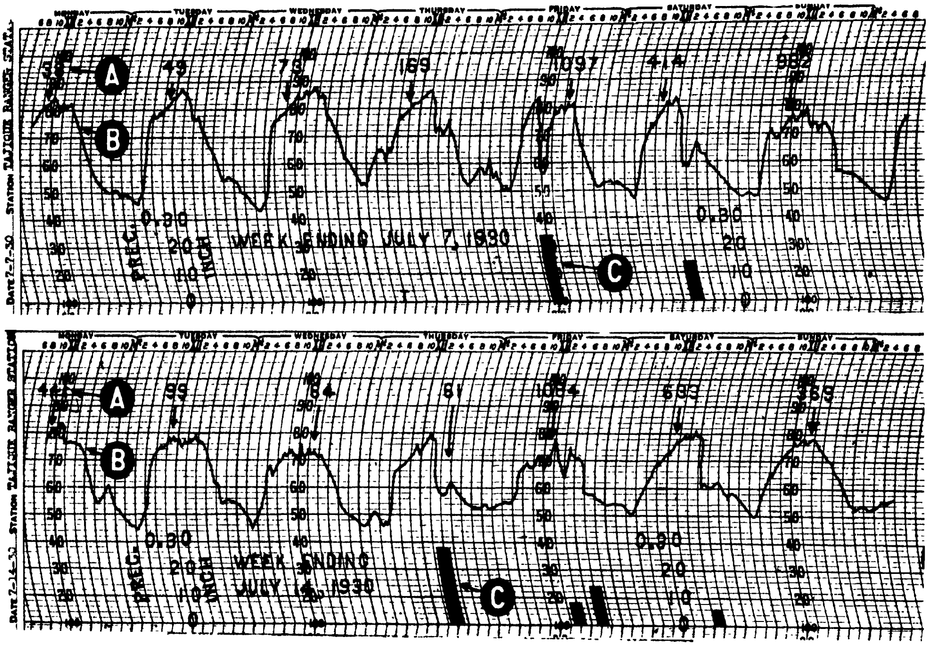

FIG. 3. Emergence of Mexican bean beetles from hibernation cages from June 30 to July 14, which includes the two periods of intensive emergence. *A*, number of beetles removed (the arrow points to the average time of removal); *B*, temperature; *C*, precipitation.

The rain of July 10 fell late in the afternoon and decreased the temperature from 79° to 57° F. The beetles were removed from the cages during the period of low temperature which followed the rain. Sixty-one beetles were removed between 4.50 and 5.20 P.M. On July 11 the temperature increased to 77° F., emergence was accelerated, and 1,084 beetles were removed from the above cages.

Few beetles emerge from the effect of temperature alone, as shown in figure 2 for June 20, 28, and 29. Table I shows that the weekly period ended June 30 was warmer and drier than the following period ended July 7. During the first period 616 beetles, or 7.55 per cent of those emerging during the whole season, emerged, whereas during the second period 3,225 beetles, or 39.52 per cent emerged.

EMERGENCE FROM NATURAL HIBERNATION

Location of Fields

Data upon emergence of the beetles from natural hibernation were obtained by recording the number of beetles in two isolated fields. Field No. 1 was located in Tajique Canyon, 1 mile below the nearest hibernation cage, and comprised an area of 0.34 acre. Field No. 2 was 3 miles northeast of the foothill cages in the fork of Canyon de la Mula and Afuera Canyon and consisted of 1,200 feet of row. Both fields were near the lower edge of the western yellow pine forest zone, the beetles' natural hibernation quarters.

The meteorological records were secured by a cooperative observer of the U. S. Weather Bureau located one-half mile below field No. 2.

Observations

The first beetles of the season were recorded in field No. 1 on June 2 (fig. 4). A rainfall of 0.29 inch over the Tajique Canyon area on May 31 stimulated a few beetles to emerge. There were general increases in the number of beetles from June 2 to 11, when 34 insects were noted in the field. On the latter date there was a precipitation of 0.01 inch and by June 13 the number of beetles had increased to 56. On June 16, 0.07 inch of rain fell over the drainage area of this canyon and stimulated emergence, with the result that the number of overwintered beetles increased to 135 on June 16, and to 249 on June 18, and to 390 on June 20. From June 20 to July 3 there was little change in the infestation. At times the number of beetles migrating out of the field down the canyon was greater than the number entering the field. The 0.24 inch of rain on July 4 stimulated a large number of beetles to leave their winter quarters for the fields. The number of overwintered beetles increased from 612 on July 3 to 3,840 on July 5, when the peak was reached. As this number taxed the small plants to their capacity, there was a rapid decrease thereafter.

The infestation of overwintered beetles in the fork of Canyon de la Mula and Afuera Canyon increased from 7 on June 16 to 144 on June 18, and from 280 on June 27 to 796 on July 1 (fig. 5). Showers fell in the canyons from July 2 to 5, inclusive, and were followed by a rapid increase in the number of beetles that entered the field. The number of beetles increased from 763 on July 3 to 1,604 on July 5, and to 3,627 on July 8. From July 8 to 12, inclusive, there was little change in the infestation. On July 15 heavy rains fell over the foothills, and an increase in infestation resulted. The peak was reached on July 16, when 4,381 beetles were recorded. This large number soon depleted the bean foliage, and a rapid decrease in the overwintered beetles followed.

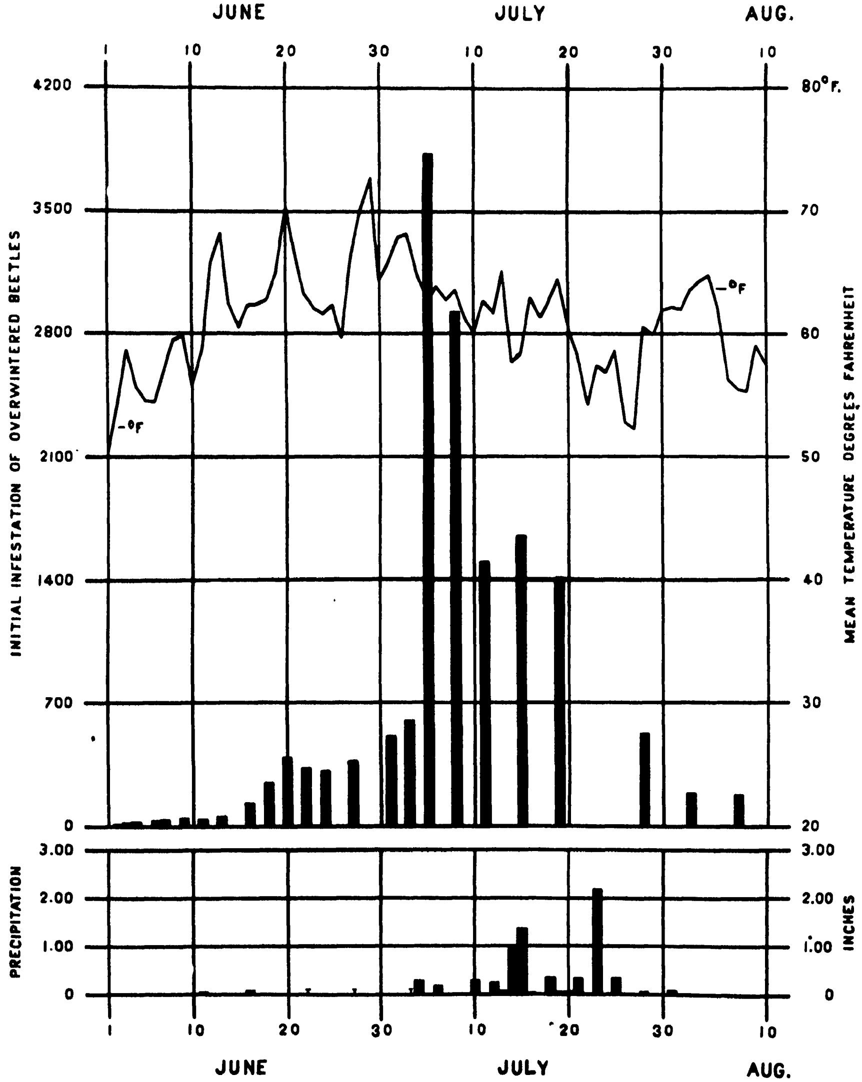

FIG. 4. Number of overwintered Mexican bean beetles appearing from hibernation on 0.34-acre bean field (No. 1) in Tajique Canyon during the season of 1930.

Figures 4 and 5 show that few beetles entered the fields during the last 10 days of June, when the temperature was the highest, and that the excessive population of overwintered beetles lasted only a short time. In field No. 1 (fig. 4) the intense infestation extended for 4 days only, from July 5 to 8, inclusive, while in field No. 2 (fig. 5) a 12-day heavy infestation occurred, from

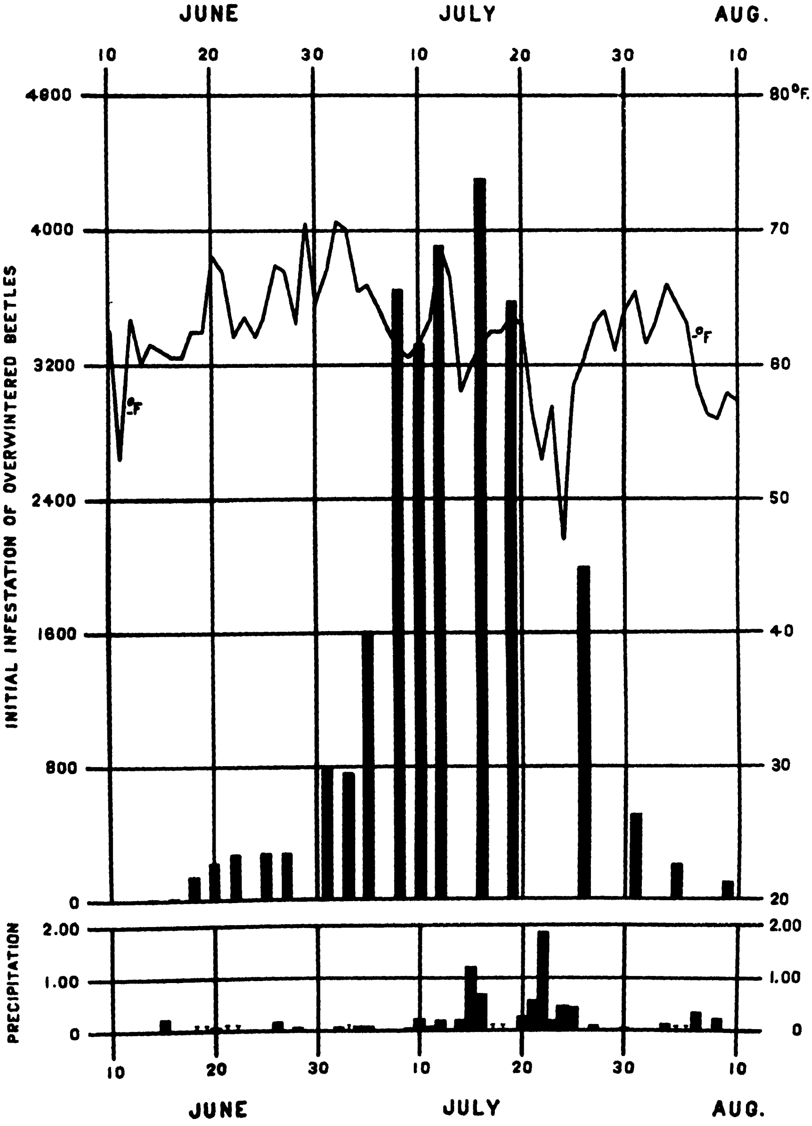

FIG. 5. Number of overwintered Mexican bean beetles appearing from hibernation on 1,200 feet of row in a bean field (No. 2) located in the fork of Canyon de la Mula and Afuera Canyon during the season of 1930.

July 8 to 19, inclusive. Thus the intensity and period of initial infestation of overwintered beetles differ slightly in different locations.

COMPARISON OF EMERGENCE IN THE CAGES AND IN THE FIELDS

The first permanent emergence from hibernation in the cages was on May 31, whereas the first beetles were seen in the field on June 2. The peaks of intensive emergence from cage hibernation occurred on July 4 and 11 (fig. 2), and the infestation of overwintered beetles in the fields was heaviest on July 5 and 16 (figs. 4 and 5). The appearance in the field subsequent to emergence from the hibernation cages is readily understood, as some time is required for the beetles to enter the fields after they have emerged from natural hibernation. In the fields the beetles are accumulating during the emergence from hibernation, while the beetles are removed daily from the hibernation cages and counted only once. Emergence from natural hibernation early in the season seemed to be slower than from hibernation cages, but this is explained by the fact that beetles become semi-active when conditions are favorable for emergence in the early spring (Douglass, '28) and later reenter the hibernation material.

FACTORS INFLUENCING EMERGENCE

Temperature is a factor in the emergence of the Mexican bean beetle from hibernation, as it has been observed that emergence in the spring begins during the first warm days in May, especially if there has been rainfall, as shown in figure 2 for May 25 and 31. It will be seen that emergence rarely occurs when the mean temperature is below 50° F. and that it attains its maximum above 60° F. If precipitation occurs on a day of normal or low temperature and the temperature rises on the following day, the number of beetles emerging will be greater on the second day, as on May 25 and 31, and June 11 and July 10. Where precipitation occurs on a day of high temperature, and a day of lower temperature follows, the number of beetles emerging the first day will be greater than on the second day, as shown in figure 2 for July 4 and 6.

Figure 2 shows that no major emergence occurred without the aid of precipitation, which indicates that precipitation is the initial stimulus although temperature accelerates emergence. The effect of precipitation on emergence is best illustrated by the data presented in figure 3, which show that, of the two stimuli influencing the issuing of the Mexican bean beetle from hibernation, rainfall is the limiting factor. By comparing the temperature, rainfall, and the number of beetles emerged from June 30 to July 3 (Monday to Thursday), inclusive, with that of July 4 to 7 (Friday to Monday), inclusive, it is found that the average temperature for the first period of four days was 66.6° F., with only a trace of rainfall, which resulted in the emergence of 329 beetles. The average temperature for the second period of four days was 63.6° F., with 0.38 inch of rainfall that stimulated 2,934 beetles to emerge. The first period may again be compared with another period of four days—

from July 10 to 13 (Thursday to Sunday), inclusive. The average temperature of this period of four days was 62.3° F., with 0.45 inch of rainfall that stimulated 2,147 beetles to emerge. During the first period the temperature was higher than during the other two periods and yet only a few beetles emerged, while during each of the periods more than 2,000 beetles emerged when there was rainfall. Local showers during the warmest part of the day will bring out of hibernation more beetles than the same amount of precipitation at lower temperatures. On July 4, 0.24 inch of rainfall with a rising temperature stimulated 1,097 beetles to emerge, as compared with July 10, when 0.28 inch of rainfall with a decreasing temperature stimulated only 61 beetles to issue. The beetles were stimulated by the shower on the afternoon of the 10th, but the decreasing temperature retarded emergence. The higher temperature of July 11 accelerated emergence with the result that 1,084 beetles emerged. On July 4 the temperature rose to 80° F., immediately after the shower, whereas on the 10th it continued to fall after the shower.

Effect of Artificial Precipitation on Emergence

To determine the effect of artificial precipitation on emergence, a cover was placed over cage No. 6 and muslin was placed at the sides to keep out all natural precipitation. This shelter was placed over the cage on May 3 during the emergence season of 1927, and on May 10 during the 1928 and 1929 season, but in 1930 the shelter was not used. After each emergence season was over, the shelter was removed.

Once or twice during the emergence season, during the hottest part of the day, water approximating 1 inch of precipitation was sprinkled into the cage with a garden sprinkler to simulate rainfall. The beetles responded quickly to the moisture stimulus, as the majority emerged within an hour after the water was applied.

Cage No. 7 was used as the check, as both cages Nos. 6 and 7 were situated on an eastern slope exposure and were about 150 yards apart.

During the fall of 1926, 1,500 beetles were introduced into cage No. 6 and 15,000 into cage No. 7. During the following falls 2,500 and 10,000 beetles were placed in cages 6 and 7, respectively.

The stimulating effect of precipitation on emergence is well illustrated in table II. During the emerging season of 1927 the peak of emergence from cage No. 7 was on June 16, when 15.94 per cent of the total number of beetles emerging during the spring and summer emerged from the effect of 0.22 inch of precipitation. On June 23, and again on July 15, 1 inch of water was sprinkled into cage No. 6 and 35.44 and 34.47 per cent of the beetles emerged, respectively. The peak of the emergence from cage No. 7 in 1928 was on July 10, when 16.96 per cent of the beetles emerged owing to the stimulating effect of 0.11 inch of rainfall. On July 30, when 0.29 inch of rain fell over this area, all the beetles in cage No. 7 had previously emerged. On the following day (July 31) when 1 inch of water was applied to cage No. 6, 59.50

TABLE II. *A comparison of emergence from hibernation on days of artificial and natural precipitation*

Date	Mean temperature ° F.	Precipitation		Beetles emerging from			
		Artificial, cage No. 6 Inch	Natural, cage No. 7 Inch	Cage No. 6		Cage No. 7	
				Number	Per cent	Number	Per cent[1]
1927							
June 16......	54.0	0.00	0.22	3	1.46	388	15.94
23......	59.0	1.00	T.	73	35.44	46	1.89
July 15......	67.0	1.00	T.	71	34.47	48	1.92
1928							
July 10......	63.5	0.00	0.11	2	1.65	39	16.96
July 30......	63.0	0.00	0.29	1	0.83	0	0.00
31......	62.0	1.00	T.	72	59.50	0	0.00
1929							
July 1......	63.0	1.00	0.47	20	52.63	28	7.82
11......	59.0	0.00	0.13	6	15.79	117	32.68
1931							
July 4......	61.8	0.00	0.05	5	11.63	110	22.40
21......	63.2	1.00	0.32	28	65.12	0	0.00

[1] Per cent of total emergence during spring and summer.

per cent of the beetles emerged. In 1929 the artificial precipitation was applied to cage No. 6 on July 1, with the result that 52.63 per cent of the beetles emerged, as compared with 7.82 per cent in cage No. 7, which received 0.47 inch of natural precipitation during the preceding night. During the emerging season of 1931 the peak of emergence from cage No. 7 occurred on July 4, when 0.05 inch of rainfall occurred. This precipitation, combined with the showers of the preceding 3 days, stimulated 22.40 per cent of the beetles to emerge. After the emerging season was over in cage No. 7, 1 inch of water was sprinkled into cage No. 6, with the result that 65.12 per cent of the beetles emerged.

It was assumed that the atmospheric moisture in the two cages was similar at the same time, being, of course, greater during periods of rainfall. That contact moisture is a greater stimulant to emergence than atmospheric moisture is shown by the fact that on June 16, 1927, 1.46 per cent emerged from the effect of atmospheric moisture (cage No. 6) as compared with 15.94 per cent as a result of contact moisture (cage No. 7). Again, on July 10, 1928, 1.65 per cent emerged from the effect of atmospheric moisture as compared with an emergence of 16.96 per cent due to contact moisture.

The effect of atmospheric moisture on emergence is well illustrated by the following data: On July 11, 1929, 0.13 inch of precipitation fell over the area, with the result that 15.79 per cent of the beetles emerged in cage No. 6. Again, on July 4, 1931, 0.05 inch of rain fell, with the result that 11.63 per cent of the beetles emerged in cage No. 6.

CONCLUSIONS

Precipitation is the limiting factor in New Mexico in stimulating emergence of the Mexican bean beetles from hibernation.

Permanent emergence rarely occurs when the daily temperature is below 50° F.

Rainfall is the initial stimulus and temperature accelerates the emergence of the beetles.

The temperature during rainfall and subsequent thereto is important; increasing temperature accelerates and decreasing temperature retards emergence.

Appearance in the field is closely associated with emergence from the hibernation cages and emergence can be correlated with rainfall.

The peak of the overwintered beetle infestation in the field is subsequent to the peak of emergence from the hibernation cages.

The stimulating effect of contact moisture is greater than that of atmospheric moisture.

Where natural precipitation is excluded, beetles may be stimulated to emerge at will by supplying water to simulate rainfall after the mean temperature has risen above the threshold of activity.

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NATIVE VEGETATION IN THE PRAIRIE HAY DISTRICT OF NORTH CENTRAL NEBRASKA[1]

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The purpose of this paper is to show the variations in structure and yield of the native vegetation as affected by depth of the ground-water table and to present typical illustrations of several plant communities contributing to the production of prairie hay. The existence of a number of distinctive plant communities is due largely to two variable factors, the ground-water table and the soil texture.

Location

The study was carried on in four counties located in north central Nebraska, the most prominent prairie hay producing section in the state. This includes the broad, reasonably level Elkhorn valley, much of which is utilized for the production of prairie hay, and a representative section of the sandhill region devoted almost entirely to grazing and the production of hay. The sandhill region is characterized by rolling hills intermingled with valleys. The latter range in size from small proportions to one mile in width and three or four miles in length.

Environmental Conditions

The annual precipitation of this region is about 23 inches. Most of the rainfall comes during the growing season. Evaporation is not especially high. There are wide fluctuations in temperature during the summer months from the relatively cool nights to the frequently hot days. The sparsely covered sandy soils of the hills respond readily to these temperature extremes. These wide fluctuations are greatly reduced in the heavier, more mesophytic soils of the valleys, which are covered with a dense growth of vegetation.

This region is largely characterized by coarse-textured soils. The hills are for the most part dune sand. The valley soils include dune sand, sand. loamy sand, sandy loam, and fine sandy loam. The subsoils are largely sand, lying from a few inches to three feet below the surface soils. The Elkhorn valley introduces a greater diversity of soil types. The more sandy types predominate but areas of heavier soils such as the loams and silt loams occur.

Water disappears rapidly in the coarse soils as a result of rapid percolation and accumulates in a well-defined ground-water table. The valley basins often dip below the water table with the resulting appearance of numerous

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marshes, ponds, and even lakes. Consequently even where the water table does not rise above the surface, it is sufficiently close to it to be of value to the vegetation. This latter fact was readily visualized by the type of vegetation present in the valleys, after the relationship between the depth of the water table and the corresponding type of vegetation was established.

The depth of the water table fluctuates from season to season and from year to year, depending largely upon the amount of rainfall. Numerous readings taken over a period of three years in definitely located water holes opened with an auger indicate that the water level fluctuates approximately three feet during the year. The highest mark is usually reached during the spring months, from March to June. The water level then gradually recedes, reaching its lowest level from September to November, after which it rises until the following spring.

According to Condra ('15) there are fluctuations in the size and depth of the lakes and ponds during wet and dry years. He concludes, also, that many bodies of water are intermittent in character because of the rise and fall of the water table.

GENERAL SURVEY OF THE VEGETATION

Pool ('14) presents a thorough discussion of the botanical structure of the sandhill vegetation. He reviews the work of numerous publications dealing with vegetation in that region of Nebraska prior to 1914. He clearly outlines and discusses the existing plant formations and associations as identified at that time. The major effect of the sandhill environment upon the existing vegetation is emphasized. According to Shantz and Zon ('24) this region lies on the western edge of the tall grass (prairie grassland) area. Keim, Frolik, and Beadle ('32) have reported on studies of prairie hay in north central Nebraska.

It is generally recognized by plant ecologists today that this section of the state lies in the mixed prairie association of the grassland formation. However, only occasional areas of the typical climax vegetation, *i.e.*, the mixed prairie association, are found in this region. The xeric condition of the rolling dune sand is holding the vegetation in a developmental state, including a number of stages with respect to climax maturity. This depends largely upon the extent to which an area of dune sand has been stabilized and covered by vegetation. The favorable mesic conditions of the wet and subirrigated valleys results in thousands of acres of vegetation in the subclimax type, largely tall grass prairie. This vegetation is comparable to that of eastern Nebraska and Iowa. Consequently one is impressed with the continuity of the natural herbaceous vegetative cover over the area, but within this complex mass are striking differences in the structure, aggressiveness, and density of the native vegetation.

Within the valleys, variations in the native vegetation are very marked, particularly to the botanist. A definite correlation exists between the structure of the vegetation and the depth at which the water table lies. This statement must take into consideration the fact that the water table fluctuates about three feet during the year.

METHODS

The weight-list method (Hanson and Love, '30) was used in determining the relative percentages of the component species. The vegetation was harvested at a uniform height with grass shears from meter quadrats. It was oven-dried and the yields calculated to a 15 per cent moisture basis. From one to ten quadrats were used for each result indicated. All yield determinations were computed to an acre yield basis. It is felt that the clipping method is comparable to commercial methods of harvesting. The more common species of grasses were separated and their relative percentage determined, while those of minor importance were recorded collectively as miscellaneous grasses. It was intended to emphasize those grasses which are of major importance to the hay producers. Sedges and rushes were combined into one group because of the difficulty in identifying the component species in the vegetative stage. The forbs, nearly all of which are considered undesirable foreign material by the commercial trade, were included as one group of plants. The vegetation of a number of areas representing each community discussed was harvested, but only one representative community is presented.

The depth of the ground-water table was determined by boring with a 4-inch auger in the immediate vicinity of the quadrats. Readings were then taken by inserting a gauge.

RELATION OF STRUCTURE OF NATIVE VEGETATION TO THE DEPTH OF THE GROUND-WATER TABLE

Table I presents a typical illustration of the relationship between kind of vegetation and depth of the ground-water table. A complete transition in this instance is made from the wet areas with the water level within a foot of the surface on June 21 to the xeric habitat with the water level over 5 feet below the surface. The *Polygonum-Phalaris* vegetation in the low, wet habitat is in turn replaced by the dominants *Spartina michauxiana, Andropogon furcatus, Sorghastrum nutans, Andropogon scoparius,* and lastly the climax *Stipa-Bouteloua* vegetation of the xeric habitat. Definite stages in succession are clearly outlined through this contiguous arrangement of dominants. There is also a consistent decrease in yield with the increasing depth of the water level.

One is impressed with the innumerable illustrations in the valleys of this area of the transitions from the hydric vegetation to the more xeric types. This includes areas representing from only one or two stages in succession to complete transitions from the hydric vegetation to the *Stipa-Bouteloua* climax type. The sandhills contain numerous stages in succession, but seldom the climax vegetation.

TABLE I. *Structure and yield of a native plant area and the relative yields of component species in relation to depth of ground-water, June 21, 1928*

Species	Depth to ground-water level (inches)									
	7.0		18.0		28.0		47.0		62.0	
	Yield per acre (15 per cent moisture)									
	Lbs.	P.ct.	Lbs.	P.ct.	Lbs.	P.ct.	Lbs.	P.ct.	Lbs.	P.ct.
Dasytephana spp.	459.6	11.3	—	—	—	—	—	—	—	—
Polygonum muhlenbergii	257.1	6.3	349.4	10.1	—	—	—	—	—	—
Phalaris arundinacea	2067.3	50.8	—	—	—	—	—	—	—	—
Alopecurus geniculatus	413.4	10.2	56.7	1.6	—	—	—	—	—	—
Phleum pratense	56.7	1.4	1752.5	50.5	185.8	10.7	28.4	1.8	—	—
Stachys palustris	35.6	0.9	—	—	—	—	—	—	—	—
Spartina michauxiana	—	—	417.6	12.0	—	—	—	—	—	—
Equisetum spp.	—	—	36.7	1.1	—	—	—	—	—	—
Hordeum jubatum	—	—	94.5	2.7	—	—	—	—	—	—
Andropogon furcatus	—	—	69.3	2.0	187.9	10.9	48.2	3.1	—	—
Melilotus alba	—	—	25.2	0.7	655.9	37.9	215.2	13.8	—	—
Sorghastrum nutans	—	—	—	—	130.1	7.5	98.6	6.3	—	—
Poa pratensis	—	—	—	—	167.9	9.7	475.4	30.5	—	—
Sporobolus cryptandrus	—	—	—	—	64.0	3.7	18.9	1.2	130.1	20.1
Elymus canadensis	—	—	—	—	55.6	3.2	8.4	0.5	—	—
Koeleria cristata	—	—	—	—	71.4	4.1	4.2	0.3	11.5	1.8
Panicum virgatum	—	—	—	—	—	—	5.3	0.3	—	—
Andropogon scoparius	—	—	—	—	—	—	471.2	30.3	59.8	9.2
Stipa spartea and *S. comata*	—	—	—	—	—	—	—	—	234.0	36.1
Bouteloua oligostachya and *B. hirsuta*	—	—	—	—	—	—	—	—	51.4	7.9
Sedges and rushes	777.6	19.1	532.0	15.3	200.5	11.7	48.2	3.1	122.8	18.9
Miscellaneous grasses	—	—	—	—	—	—	2.1	0.1	11.5	1.8
Miscellaneous forbs	—	—	136.5	3.9	9.4	0.5	133.3	8.6	27.3	4.2
Total	4067.3	100.0	3470.4	100.0	1728.5	100.0	1557.4	100.0	648.4	100.0

The valleys are covered for the most part with earlier stages of the hydrosere, while the hills are supporting largely developmental stages of the xerosere.

MAJOR PLANT COMMUNITIES

The Climax Stipa-Bouteloua Community. A typical plant community of the climax vegetation is presented in table II. The water table was too deep

TABLE II. *Structure and yield of a climax Stipa-Bouteloua area. July 2, 1926*[1]

Species	Yield per acre (15 per cent moisture)	
	Pounds	Per cent
Stipa spartea	270.7	20.4
Bouteloua oligostachya	399.8	30.2
Andropogon scoparius	135.4	10.2
Koeleria cristata	90.2	6.8
Andropogon hallii	44.1	3.3
Calamovilfa longifolia	38.8	2.9
Panicum virgatum	28.3	2.1
Sorghastrum nutans	11.5	0.9
Miscellaneous grasses	74.5	5.6
Sedges and rushes	108.1	8.2
Forbs	123.9	9.3
Total	1325.3	100.0

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[1] The data in tables II and IV were collected by G. W. Beadle, formerly graduate assistant in the Department of Agronomy.

to have any favorable influence on the vegetation. The soil was of a loamy sand type.

Stipa and *Bouteloua* are the dominants on the heavier upland soils of this region. Other species often occupy a prominent place in some plant communities, a number of them serving in the rôle of subdominants. The following graminaceous species are of considerable importance in prairie hay harvested from this type of meadow: *Stipa spartea, S. comata, Bouteloua hirsuta, B. oligostachya, Andropogon scoparius, Koeleria cristata, Andropogon hallii, Calamovilfa longifolia, Sporobolus cryptandrus,* and *Panicum virgatum.*

Vegetation of this type covers hundreds of acres consisting principally of knolls in the Elkhorn valley and adjacent heavier soils adjacent to the valley. This climax vegetation, however, is of minor importance in the sandhills.

The Subclimax Tall Grass Community. The data in tables III and IV are illustrative of the subclimax vegetation of the more favorable environment in the wet and subirrigated valleys. The vegetation as presented in table III was on a sandy loam type of soil with the water table at a depth of 33 inches on August 12. The area introduced in table IV contained a silt loam surface soil with the water table at 45 inches on July 6. Vegetation of the type included in table III is indicative of the low wet areas where the water level

TABLE III. *Structure and yield of a hydrophytic tall grass area. August 10, 1929*

Species	Yield per acre (15 per cent moisture)	
	Pounds	Per cent
Spartina michauxiana	692.5	20.9
Calamagrostis canadensis	711.5	21.5
Calamagrostis neglecta	432.3	13.1
Poa pratensis	342.1	10.3
Phalaris arundinacea	61.9	1.9
Phleum pratense	61.9	1.9
Puccinellia airoides	15.8	0.5
Hordeum jubatum	10.5	0.3
Agropyron tenerum	1.1	0.1
Sedges and rushes	579.4	17.5
Forbs	398.7	12.0
Total	3307.7	100.0

TABLE IV. *Structure and yield of a subirrigated subclimax tall grass area. July 6, 1926*

Species	Yield per acre (15 per cent moisture)	
	Pounds	Per cent
Andropogon furcatus	372.6	17.9
Sorghastrum nutans	868.8	41.6
Phleum pratense	133.3	6.4
Sporobolus spp.	84.0	4.0
Panicum virgatum	42.0	2.0
Spartina michauxiana	19.9	1.0
Elymus canadensis	12.6	0.6
Trifolium spp.	38.7	1.9
Miscellaneous grasses	136.3	6.5
Sedges and rushes	274.9	13.2
Forbs	103.9	5.0
Total	2087.0	100.0

stands at, above, or within a few inches of, the surface for a number of weeks in the spring and early summer.

Spartina michauxiana, accompanied by the sedges and rushes, is decidedly the most common species in the wet habitat. These species invariably compose a large percentage of the Midland hay as provided for in the *Handbook of Official Hay Standards* for government grades of prairie hay. Other species worthy of mention as being at least of some importance in prairie hay are as follows: *Calamagrostis neglecta, C. canadensis, Phalaris arundinacea, Alopecurus geniculatus,* and *Panicum virgatum.*

Plant communities of this structure usually occupy irregular, restricted areas about lakes, ponds, marshes, and streams and low areas in valleys not containing bodies of water.

Two cultivated species *Phleum pratense* and *Poa pratensis* are represented as component species in the vegetation of table III, and the former also in table IV. Many attempts have been made by hay producers to introduce by seeding a number of cultivated species and so to increase the productivity of the native meadows and as a result a number of these species have been successfully established on much of the wet and subirrigated land. The increase and successful establishment of those species in many meadows other than those seeded has been a result of natural reseeding and subsequent dissemination of the seed by haying machinery and livestock. *Phleum pratense* and *Poa pratensis* are especially good illustrations of this successful invasion with the result that they occur as component species in varying degrees of importance in thousands of acres of valley terrain.

Vegetation of the kind listed in table IV is illustrative of a much larger acreage of valley hay land, viz, the bluestem meadows. Thousands of acres of land have the ground-water level sufficiently close to the surface to provide the bluestem vegetation but not too close to bring about the presence of the more hydrophytic vegetation as discussed in connection with the wet areas. The bluestems, *Andropogon furcatus* and *Sorghastrum nutans,* are decidedly the dominants in this type of plant community. *Andropogon scoparius* often plays an important rôle. Other native species occurring in this meadow type and contributing materially to prairie hay are *Spartina michauxiana, Panicum virgatum, P. scribnerianum, Andropogon tenerum, A. smithii, Elymus canadensis, Sporobolus* spp., and *Sphenopholis obtusata.* The introduced species *Poa pratensis, Phleum pratense,* and *Agrostis alba* also play an important rôle.

This vegetation covers a large percentage of the acreage harvested for prairie hay. Nearly all of the subirrigated valleys, including the Elkhorn, are largely covered with bluestem type of vegetation.

The Subclimax Sandhill Successional Communities. The dune sand hills are for the most part covered with a sparse growth of vegetation, characteristic of successional types. Numerous stages exist, depending upon the extent to which the dune sand has been stabilized by the vegetative cover. Along with the foremost species, such as *Muhlenbergia pungens* and *Red-*

fieldia flexuosa, which are among the primary invaders in the sand "blowouts," other species enter in turn as the habitat becomes more favorable. A number of these species assume the rôle of dominants in turn of their invasion. Species worthy of mention because of their relative prominence are *Calamovilfa longifolia, Stipa comata, Bouteloua hirsuta, Sporobolus cryptandrus, Andropogon scoparius, A. hallii, Panicum wilcoxianum, P. virgatum,* and *Eragrostis trichodes.*

Table V illustrates a community which has profoundly stabilized the habitat. The water table was situated at such a depth as to be of no consequence to the vegetation. The plants were growing in dune sand containing a small accumulation of organic matter. All species appearing as dominants in previous stages are still present even though of minor importance at this stage of development.

TABLE V. *Structure and yield of a characteristic dune sand area covered with sandhill successional vegetation. August 9, 1929*

Species	Yield per acre (15 per cent moisture)	
	Pounds	Per cent
Calamovilfa longifolia	678.9	48.8
Stipa spp.	98.6	7.1
Sporobolus cryptandrus	37.8	2.7
Panicum virgatum	37.1	2.6
Andropogon scoparius	26.2	1.9
Andropogon hallii	18.9	1.4
Bouteloua hirsuta	17.8	1.3
Muhlenbergia pungens	14.7	1.0
Panicum wilcoxianum	6.2	0.4
Redfieldia flexuosa	5.3	0.4
Festuca ovina	1.1	0.1
Sedges and rushes	18.9	1.4
Forbs	430.2	30.9
Total	1391.7	100.0

DISCUSSION AND CONCLUSIONS

Two factors have a profound effect upon the structure of the herbaceous vegetation cover of north central Nebraska. One factor is the xeric environment over much of the terrain as a result of the coarse textured soils, viz., the sandhills, and the second factor is the mesophytic conditions of the wet and subirrigated valley land. Consequently only limited areas of the *Stipa-Bouteloua* climax vegetation are to be found. All stages of successional vegetation of the xerosere in the uplands and of the hydrosere in the valleys exist.

A striking contrast in the structure and yield of the native vegetation may be brought about as a result of variation in the depth of the underlying ground-water table. Changes of only a very few feet in the depth of the water table have a profound effect on the type of vegetation. A variation in depth of the water table of five feet or more, which is usually accompanied by a variation in the coarseness of the soils, may induce a complete change in the type of vegetation, such as from a *Phalaris-Polygunum* type of vegetation to the *Stipa-Bouteloua* climax type. Yields are decreased accordingly with the climax vegetation yielding only a fraction as much as the mesophytic vegetation.

A number of plant communities are the basis of the prairie hay industry. The slough grass-sedge community makes up a large part of the prairie hay classified as " Midland " according to the government grades. This type of vegetation constitutes a minor yet an important phase of the prairie hay produced in this region. The bluestem communities, however, are the basis of the successful prairie hay industry. These occupy well over fifty per cent of the acreage of meadow lands harvested for hay. Both the yields and the quality of hay make these areas the best from the hay producer's viewpoint.

The vegetation introduced in connection with dune sand and the uplands is important with respect to acreage. The accompanying xeric environment supports the poorest types of plant communities in terms of the hay industry. The lack of subirrigation water, accompanied by the coarse-textured soils, provides a habitat in which only the more xeric species can become established. These include grasses which yield a small quantity of hay of inferior quality. This hay usually consists of an appreciable quantity, approximately 30 per cent, of forbs, which are of little feeding value.

Most of the upland terrain is utilized for grazing. These xeric plant communities are harvested only occasionally by hay producers but those haymen not having a sufficient acreage of the desirable haylands are often forced to harvest the poor meadows. A scarcity of hay during lean years or attractive prices are often an inducement to harvest a larger acreage of the upland meadows than under normal conditions.

The farmers in general have learned to note differences in the complex vegetative cover. They have partially solved their problems with respect to efficient means of handling this land, using the vegetation as an indicator.

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ACTIVITY OF BLOWFLIES AND ASSOCIATED INSECTS AT VARIOUS HEIGHTS ABOVE THE GROUND

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When one is working with insect traps, baits and repellents, it is important to know the responses at different heights above the ground of the insect being studied. Questions arise as to whether an insect trap for certain pests should be placed near the top or in the center of a tree, whether a flytrap could be set more advantageously on top of a windmill tower than on the ground, or at what level status tests for insects should be made.

In April, 1930, while a study was being made of the status of blowfly parasites in different localities, interference with the baits by dogs necessitated the placing of the bait containers in trees. It was suggested that the increased height might affect the extent of parasitism. To determine this a test was made at Uvalde, Texas, in which jars containing meat were exposed at various levels, permitting blowflies and their associated insects to breed in the meat. This test was begun in June, 1930, and continued until September; it was repeated during the same months in 1931.

The author is indebted to the following specialists for determination of specimens: Diptera, J. M. Aldrich, E. W. Laake, David G. Hall; Hymenoptera, A. B. Gahan; and Coleoptera, E. A. Chapin, H. S. Barber, W. S. Fisher.

APPARATUS

In order to provide means for placing the baits, an oak tree 30 feet high was selected and in this tree a pole was erected so that the tip of the pole was 45 feet above the ground. Metal pulleys and cotton sash rope permitted the raising and lowering of the jars.

These pint mason jars were filled to a depth of 1½ inches with sifted sand on which four ounces of meat were placed. During exposure the jars were capped with lids of 4-mesh hardware cloth, a size which allowed the entry of all flies and predatory beetles but excluded birds, mice, and other animals. At the conclusion of the exposure these lids were exchanged for tops of 60-mesh brass strainer cloth.

The jars were placed in holders during exposure. These holders protected the baits from rain and, to some extent, from the sun, and enabled the jars to be elevated into position. The top and bottom of the wooden holders were each 3¾ inches square, and these were connected by side slats 1½ inches wide and 8 inches high. A metal ring in the top of the holder permitted attachment to the hoisting rope. The jars were held in the holders by means of wires.

Location of the Baits

The experiment was conducted on a mesquite flat with abundant grass, dense areas of weeds, and underbrush about 10 feet high. The oak tree was one of several growing in the immediate area.

The baits were exposed at four heights on the east side of the tree trunk or pole, thereby being somewhat protected from the afternoon sun. Below is a brief description of each position:

(1) At the ground, shady, with morning sun, dense weeds nearby but immediate location open and air circulation good.

(2) Fifteen feet above the ground, in about the center of the tree, broken shade from limbs and foliage, fairly open location, air circulation good.

(3) Thirty feet above the ground, level with topmost branches, no protection from sun other than top and sides of jar holder.

(4) Forty-five feet above the ground, no protection other than jar holder.

Experimental Procedure

In 1930 the first set of four baits was exposed on June 20, and at the end of 10 days they were replaced by the second set. A series of 10 sets was thus exposed during the season, the last set being brought in September 28. In 1931 another series of 10 sets was exposed beginning on July 1 and ending October 8.

The baits were prepared at the laboratory. Four ounces of meat from a newly killed rabbit were placed in each jar, which was then capped with a solid metal lid to exclude insects. At the exposure station the solid lids were replaced by the 4-mesh tops. Upon collection the jars were capped with 60-mesh tops.

The numbers of flies refer to the numbers emerging from larvae which bred from the meat and pupated in the sand in the jars. The emergence from these jars was recorded each day, and the material kept in the insectary for sixty days to insure emergence of all insects.

Data on the blowfly parasites show the number of adult parasites which emerged from blowfly larvae and pupae parasitized within the jars. The percentage of parasitism is based on the number of flies and parasites which emerged. *Brachymeria fonscolombei* (Dufour) is a solitary larval parasite; therefore each adult of *B. fonscolombei* which emerged represents one fly destroyed. On the other hand, *Mormoniella vitripennis* (Walk.) is a pupal parasite, more than one parasite issuing from a host pupa. At Uvalde, Tex., an average of 36 *M. vitripennis* was found to emerge from a single pupa of *Sarcophaga plinthopyga* Wied. and smaller species of flies produce smaller numbers of this parasite. Of the flies which emerged in this experiment 83 per cent were Sarcophaga. Considering that the remaining 17 per cent were smaller flies, the average emergence of *M. vitripennis* from a single pupa would be less than 36. An average of 30 *M. vitripennis* per pupa was estimated, although this figure is probably high. In the tables after each figure for *M. vitripennis* the estimated number of blowfly pupae killed is given in parenthesis. This figure was the one used in computing the percentage of parasitism.

The number of beetles was determined at the time of collection by removing and counting the specimens of every species in each jar. In two tests in 1930 the beetles were not counted; therefore the data for that year are based on eight while the 1931 data comprise ten tests.

No attempt was made to study the variations in temperature, humidity, or other environmental factors at the different heights, although it was evident that they existed. Temperatures (Fahrenheit) during the period of the test were as follows: 1930, average daily mean, July 84°, August 85°, September 82°, maximum for period 104°, minimum 59°; 1931, average daily mean, July 82°, August 82°, September 83°, maximum for period 99°, minimum 60°.

RESULTS

From the 80 baits exposed during two years' tests, 8,859 insects (2,099 blowflies, 1,823 blowfly parasites, and 4,937 predatory and meat-infesting beetles) were collected or reared. The numerical distribution of these insects as to altitude location is indicated by the number that was secured at each height. The largest number in one situation was 3,221 (36.4 per cent) at the ground, the numbers decreasing approximately in proportion to the increase in height, as follows: 2,635 (29.7 per cent) at 15 feet, 1,830 (20.7 per cent) at 30 feet, and 1,173 (13.2 per cent) at 45 feet. Table I shows the number by species of flies and parasites reared from the baits and table II shows the number of beetles of each species collected.

Blowflies

Of the total number of insects that emerged, 2,099 were blowflies. These were distributed fairly evenly among the four situations: 24.11 per cent of them were taken at the ground and 24.49 per cent at the 45-foot level; the greatest emergence was 33.35 per cent at 30 feet, and the smallest 18.05 per cent at 15 feet.

It will be seen in table II that the jars in the two lower situations caught most of the predatory beetles. The small number of flies recorded at these levels was probably due to the destruction of many blowfly larvae by these beetles. The number of parasites recorded was probably also reduced in the same way. This is indicated in the discussion of *B. fonscolombei*, where parasitism is shown to have increased with increased height, and in table I, where at 45 feet the fly emergence of 24 per cent of the total emergence was increased to 28 per cent when parasites were included.

At the ground location only 52 flies and 5 parasites were secured during the entire season of 1931. The fact that a large number of *Saprinus* beetles

TABLE I. *Blowflies and their parasites emerged from meat baits exposed at various heights above the ground, Uvalde, Texas, 1930 and 1931*

		At ground		15 feet		30 feet		45 feet		Total	
		No.	%	No.	%	No.	%	No.	%	No.	%
Flies											
Sarcophaga	1930	362		215		366		122			
spp.	1931	8		53		249		374			
	Total	370	21.16	268	15.32	615	35.16	496	28.36	1,749	83.33
Fannia	1930	8		18		67		2			
femoralis	1931	8		47		3					
	Total	16	10.46	65	42.48	70	45.75	2	1.31	153	7.29
Cochliomyia	1930	2									
macellaria	1931	36		25							
	Total	38	60.32	25	39.68					63	3.00
Synthesiomyia	1930	59									
nudiseta	1931										
	Total	59	100.00							59	2.81
Lucilia	1930	22				8		11			
hirtiforceps	1931										
	Total	22	53.66			8	19.51	11	26.83	41	1.95
Ophyra	1930	1		17							
aenescens	1931										
	Total	1	5.56	17	94.44					18	0.86
Lucilia	1930										
unicolor	1931			1		7		5			
	Total			1	7.69	7	53.85	5	38.46	13	0.62
Ophyra	1930										
leucostoma	1931			3							
	Total			3	100.00					3	0.14
Total flies by location		506	24.11	379	18.05	700	33.35	514	24.49	2,099	100.00
Parasites											
Brachymeria	1930	140		96		215		275			
fonscolombei	1931	5		114		49		97			
	Total	145	14.63	210	21.19	264	26.64	372	37.54	991	
Mormoniella	1930	796(27)[1]		36(2)							
vitripennis	1931										
	Total	796(27)[1]	95.67	36(2)	4.33					832(29)	
Total flies and parasites by location[2]		678	21.73	591	18.95	964	30.91	886	28.41	3,119	100.00

[1] Numbers in parentheses indicate the estimated number of blowfly pupae destroyed by the parasites.

[2] These totals do not include the actual number of *M. vitripennis* emerged; instead, the number of estimated host flies destroyed (29) is used.

TABLE II. *Beetles collected from meat baits exposed at various heights above the ground, Uvalde, Texas, 1930 and 1931*

		At ground		15 feet		30 feet		45 feet		Total	
		No.	%	No.	%	No.	%	No.	%	No.	%
Dermestes caninus	1930	169		295		132		13			
	1931	954		1,603		729		206			
	Total	1,123	27.38	1,898	46.28	861	21.00	219	5.34	4,101	83.07
Saprinus spp.	1930	11		1							
	1931	609		92		3		63			
	Total	620	79.59	93	11.94	3	0.38	63	8.09	779	15.78
Creophilus maxillosus	1930	1									
	1931	15		2							
	Total	16	88.89	2	11.11					18	0.37
Necrobia rufipes	1930	2		1							
	1931	2		8							
	Total	4	30.77	9	69.23					13	0.26
Canthon cyanellus	1930										
	1931	5		2				5			
	Total	5	41.67	2	16.66			5	41.67	12	0.24
Crigmus texanus	1930			3							
	1931	1				1					
	Total	1	20.00	3	60.00	1	20.00			5	0.10
Necrophorus marginatus	1930	2				1					
	1931	1									
	Total	3	75.00			1	25.00			4	0.08
Dermestes nidum	1930										
	1931	1		3							
	Total	1	25.00	3	75.00					4	0.08
Trox sp.	1930	1									
	1931										
	Total	1	100.00							1	0.02
Total by location		1,774	35.93	2,010	40.71	866	17.54	287	5.82	4,937	100.00

was collected from this location during 1931 (table II) may explain this situation.

It must be concluded, therefore, that, had it not been for predatory beetles, the greatest percentage of emerged flies would doubtless have been from the lower locations.

Sarcophaga spp. The *Sarcophaga* were not determined to species because of the difficulty of securing identifications of the little-known forms. Probably 85 per cent of them were *Sarcophaga plinthopyga* Wied. This genus constituted 83.33 per cent of the fly emergence—not an unexpected number in view of the size and kind of baits and the fact that the jar method is particularly favorable for *Sarcophaga.* The distribution by elevation was similar to that given for the total emergence of flies.

Fannia femoralis Stein. This small fly is reared frequently from meat. It did not appear active in the 45-foot baits and seemed to prefer the area within the confines of the tree.

Cochliomyia macellaria Fab. The common screw-worm fly of the Southwest is far more abundant than is indicated by its emergence figure of 3.00 per cent. During the summer months about 90 per cent of flies trapped over meat baits are *C. macellaria*. The small numbers recorded here—38 at the ground, 25 at 15 feet, and none above—were probably due to the unfavorable competition with *Sarcophaga* which occurs in small baits. These figures, though not conclusive, suggest that *C. macellaria* is a ground inhabiting species. Townsend ('28), in Illinois, trapped flies at various heights but used molasses and banana for bait. He says, "The screw-worm fly was taken only late in the summer and chiefly from the ground trap. . . . Only one was taken in the tree-tops and a few at the 25-foot level."

Synthesiomyia nudiseta V. d. W. More frequently encountered in breeding work than in fly trapping, this fly, which resembles *Sarcophaga*, constitutes from 0.5 to 2.5 per cent of the blowfly population in southwestern Texas. In these tests it was found only on the ground.

Lucilia hirtiforceps Shannon, *Lucilia unicolor* Towns. Although these species of *Lucilia* were taken in small numbers, 41 and 13, respectively, it is important to note their prevalence in the upper jars. Nearly 50 per cent of *L. hirtiforceps* and more than 90 per cent of *L. unicolor* emerged from the two upper situations. This is an indication that *Lucilia* is an inhabiter of trees and high levels as well as of the ground. Townsend ('28) also found *Lucilia* abundant in trees at 25 and 50 feet above the ground. *Lucilia unicolor,* the more abundant of the two species, is prevalent in spring, fall and winter, often representing 5 to 6 per cent of the blowfly population. Although *Lucilia sericata* Meig. is very common at Uvalde during the summer months, no specimens emerged from the baits.

Ophyra aenescens Wied., *Ophyra leucostoma* Wied. *Ophyra* is a frequently seen fly, nearly always present but in small numbers. Seldom does either of these species exceed 0.7 per cent of the fly population. They were encountered only at the lower levels in these experiments.

Parasites

Brachymeria fonscolombei (Dufour). This is a larval parasite of blowflies. Since only one parasite emerges from each host, the 991 adults emerging during the test represent 991 flies destroyed.

The abundance of *B. fonscolombei* increased with increased height, the emergence being 14.63 per cent at the ground, 21.19 per cent at 15 feet, 26.64 per cent at 30 feet, and 37.54 per cent at 45 feet.

The percentage of parasitism of flies, as indicated by the ratio between the emergence of flies and parasites, was also shown to increase with increased height. This accounts for the greater number of parasites in the upper baits. There is a discrepancy in the figures for either the 15 or the 30 foot situation, but until more data are obtained this cannot be corrected. It is probable that further tests will show the percentage of parasitism at 30 feet to be greater.

There is a question as to whether or not all the species of flies given in table I are hosts for *B. fonscolombei.* This parasite has been bred from *Sarcophaga, Cochliomyia, Synthesiomyia,* and *Lucilia.* The remaining species, all small flies, *Fannia femoralis, Ophyra anescens,* and *O. leucostoma,* should be considered. The percentage of parasitism by *B. fonscolombei* has been worked out on the basis, first, of the emergence of both parasites and all the flies, and second, of the emergence of all these except *Fannia* and the two species of Ophyra.

TABLE III. *Parasitism of blowflies by Brachymeria fonscolombei based on emergence tests*

Height in feet	% based on total emergence of flies and parasites	% based on emergence of parasites and flies except *Fannia* and *Ophyra*
45	41.99	42.08
30	27.37	29.53
15	35.53	41.50
Ground	21.39	21.94
Total *B. fonscolombei* emergence	31.77	33.65

A comparison of these figures shows little variation except at the 15-foot elevation. Future study of *Ophyra* and *Fannia* should show their exact relation to *B. fonscolombei.* In all arrangements of data in this paper the entire number of flies was used in computations.

The effect of predatory beetles on the percentage of parasitism was of no great importance, as parasite-infested and noninfested blowfly larvae are destroyed alike.

Mormoniella vitripennis (Walk.). All the blowflies under consideration are attacked by this pupal parasite. 36 *M. vitripennis* emerged from the situation at 15 feet and 796 from the jars on the ground. These represent respectively 2 and 27 blowflies destroyed. The percentage of parasitism was 0.34 per cent at 15 feet and 3.98 per cent at the ground. Johnson ('29), in discussing injury to nestling birds by *Protocalliphora,* refers to several instances of parasitism of *Protocalliphora* by *M. vitripennis* (*M. brevicornis* Ashm.). This indicates the activity of *Mormoniella* in trees, although the heights from which the nests were collected were not given nor was it stated whether or not the pupae were protected from parasites after collection.

Check Area for Activity of Parasites. During the progress of this test exposures were made in a check area surrounding the tree used in the experiment. This check consisted of 10 four-ounce meat baits exposed every 10 days over an area of a square mile. Two baits were placed in the center of the area, and one was placed at a distance of a quarter-mile and one at a half-mile in each cardinal direction. A total of 200 baits were exposed with an emergence as follows: *B. fonscolombei,* 28.52 per cent; *M. vitripennis,* 0.60 per cent; flies 70.88 per cent. The average percentage of parasitism by *B. fonscolombei* in the tests at different heights was 31.77, somewhat higher than the check figure. *M. vitripennis,* with an emergence of 0.93 per cent, was also slightly above the check.

Beetles

The 4,937 beetles collected consisted of blowfly predators and beetles associated with carrion. The numbers secured, as recorded in table II, clearly demonstrated that their greatest activity is near the ground. The two lower locations contributed 76.64 per cent of the beetles collected, with 17.54 per cent at 30 feet and only 5.82 per cent at 45 feet.

Dermestes caninus Germ. Comprising 83.07 per cent of the total number of beetles, *D. caninus,* although not a predator, must be considered in its relation to blowfly breeding. Although *Dermestes* will feed on blowfly larvae when confined alone with them, this has never been observed under normal conditions. There must, however, be some competition from these beetles, which breed in carcasses and which collect in such numbers within 10 days after exposure of baits.

Saprinus spp. (Histeridae). This genus was represented mainly by two species, *Saprinus lugens* Er. and *S. lubricus* Lec., and its closely related forms. Because of the difficulty of securing determinations of the latter species, the entire group was considered together under the generic name. They appeared more active at the ground, but 63 specimens were collected at 45 feet. This genus is the most effective group of blowfly predators in this locality.

Creophilus maxillosus L., *Necrobia rufipes* DeG., *Necrophorus marginatus* Fab. These three blowfly predators combined constituted less than 1 per cent of the total number of beetles. With one exception they were present only at the two lowest levels.

Canthon cyanellus Lec., *Crigmus texanus* Lec., *Dermestes nidum* Arrow, *Trox* sp. All these species are encountered from time to time in work with meat-breeding Diptera. Of interest in this instance was the presence of five *C. cyanellus* at 45 feet.

SUMMARY

A four-ounce meat bait was exposed at each of the four following heights: On the ground, and at 15, 30, and 45 feet above the ground. The baits remained in place 10 days and were followed by a second series. Eighty baits were exposed during 1930 and 1931. From these were reared or, in the case of beetles, collected, 8,859 insects.

The total number of insects secured in each situation decreased approximately in proportion to the increase in height.

The 2,099 flies emerging were fairly evenly distributed between the four elevations. The activity of predatory beetles in the two lowest baits probably prevented the percentage of flies from being greater at these situations.

During the 1931 tests only 52 flies and 5 parasites emerged from the baits on the ground, explained by the collection of 609 *Saprinus* beetles from this location.

Of the 1,823 parasites emerged, 991 were *Brachymeria fonscolombei* (Dufour). The numbers of this parasite, as well as its percentage of parasitization, increased with increased height. *Brachymeria fonscolombei* constituted 31.77 per cent of the emergence from the baits. In a check area the emergence of this parasite was 28.52 per cent during the same period.

Most of the 4,937 beetles collected were at the lower levels, 76 per cent being divided between the ground baits and those at 15 feet. *Dermestes caninus* Germ. comprised 83 per cent of the beetles, but this species is not an active predator of blowflies. *Saprinus* spp., the most important blowfly predators encountered, represented 15.78 per cent of the collection. Of the *Saprinus* beetles 79.59 per cent were on the ground, but 8.09 per cent were found at 45 feet.

Of the 8,859 insects involved, 1,823, or 20.58 per cent, were hymenopterous parasites; 2,099, or 23.69 per cent, were flies; and 4,937, or 55.73 per cent, were beetles. These figures are some indication of the ratio between blowflies and the insect enemies of their larval and pupal stages. They also explain to a great extent how blowflies are held in check.

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PHYTOSOCIOLOGICAL NOMENCLATURE[1]

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In the April issue of Ecology Bartlett ('33) has discussed the nomenclature of plant associations used by the majority of European geobotanists. His article, which displays its author's linguistic erudition, is a plea for the adoption in America of a phytosociological nomenclature that is pure from the point of view of language, and at the same time clear and explicit.

But—and this is the weak spot in the article in question—Bartlett takes a too exclusively linguistic stand and does not consider the question sufficiently from the point of view of plant sociology. It is with regret that we feel ourselves obliged to say that he gives the impression of not having followed the evolution of our science and its nomenclature, and in particular he seems unacquainted with the work and decisions of the Phytographic Section of the International Congress held in Brussels in 1910 (Flahault and Schröter, '10).

As we are at work on the foundations of a phytosociological index which is to cover all plant associations and describe them more or less accurately, we were glad to accept the invitation of the editors of Ecology to reply to certain critical objections made by Bartlett—objections which would seem detrimental to the development of our science.

What we are concerned with is the nomenclature of associations, subassociations, alliances and orders.

Associations.—We may name an association after one (or two) characteristic or very important species, as the *Carex curvula* association. It is often convenient for the sake of brevity to use the radical of the name of the genus or a species and add the suffix *-etum*. Bartlett accepts this suffix in the case of generic names; e.g., Pinetum, Quercetum, but he rejects it in cases where the specific name is combined with a genetive as in *Caricetum curvulae, Quercetum pubescentis,* and proposes on the contrary, as being more correct, *Caricetum Caricis curvulae, Quercetum Quercus pubescentis.* To use this is merely useless complication; we hold to the recommendations and decisions of the Brussels Congress, where the method of designating the associations, used by us, was accepted practically unanimously, there being but one vote cast against it—by Mr. Beck von Mannagetta. As regards the use of the stem of a noun denoting a species plus the termination *-etum*, as in Curvuletum (introduced by Schröter fifty years ago), we agree with

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[1] Station Internationale de Géobotanique Méditerranéene et Alpine, Montpellier. Communication No. 24.

Bartlett that it will be best to avoid this form as much as possible in future. We might, however, retain words already coined and in general use, such as *Curvuletum, Trifidi-Distichetum*—words which are entirely unequivocal; in fact, a list of *nomina conservenda* might be drawn up, in which words of this kind could then be included.

Sub-Associations.—To distinguish the sub-associations, the termination *-etosum* is added to the radical of the generic name of one of the most characteristic or most abundant species of the sub-associations, as in *Molinietum caricetosum tomentosae*—a sub-association of *Molinietum* with *Carex tomentosa.* Any one acquainted with this field and conversant with the subject of phytosociological associations, alliances, and orders will at once grasp the meaning of such a conception, after which he will find no difficulty in making use of the terms we employ in describing these. The terminology becomes more complicated in dealing with subdivisions of the associations, but this is inevitable. Of course it will be advisable not to overdo the use of the suffix *-etosum;* whenever possible ordinary language should be used (*e.g.*, sub-association of *Stellaria holostea* of the Querceto-carpinetum). There are many cases, however, in which the suffix *-etosum* may be used without the least danger of misunderstanding, as has been successfully demonstrated in the works of numerous writers.

Phytosociological Alliances.—In order to make an immediate distinction between associations and alliances (units in a higher category) we have proposed that the suffix *-ion* should be added to the stem of the name of one of the chief associations belonging to the alliance, e.g. *Ammophilion.* In pursuance of his otherwise very laudable intention of trying to purify scientific terminology, Bartlett makes a great effort to demonstrate that it would be much better to introduce the Latin suffix *-ium* instead of the Greek *-ion.*

There was a good reason for choosing the suffix *-ion.* We wished in the first place to create terms which would be short, comprehensive, and of a kind that would not lead to confusion. If we had chosen *-ium* as suffix, we should have been forced to make words too easily confused with the generic names of taxonomy. How, one may ask, shall we then distinguish between the *Brachypodion* alliance and the genus *Brachypodium,* if we adopt his suggestion? As a matter of fact, an infinitude of generic names end in *-ium,* as *Cirsium, Conium, Hieracium,* etc. This is the principal reason why we bastardized Latin words with a Greek suffix and why we cannot accept Bartlett's suggestion.

Phytosociological Orders.—To designate the orders, the suffix *-etalia* is added to the radical of the name of the principal associations of the order, *e.g., Caricetalia curvulae.* Bartlett thinks this form better from a linguistic point of view than the one used for alliances. We are glad to note his opinion. As he says, it is obvious that the word should be used in the plural, as we have done in our own works (see Braun-Blanquet and Jenny, '26). If by chance a singular has been used, this is simply due to a typographical error.

Xerobrometum, Mesobrometum. It was probably Mr. Woodhead, an Anglo-Saxon, who was the first to introduce the term *Xero-Pteridetum,* with the prefix *Xero.* His example has been followed by several authors. At the Brussels Congress Harshberger, wishing to stem the tide of association names of this kind, proposed that association names of this sort should not be accepted unless they appeared in parenthesis. (See Harshberger proposal 13.) But this suggestion was rejected by six votes to three. The majority of those voting seemed to be in favor of names with the prefix. Obviously the coining of such terms must not be overdone.

Certain of the ideas expressed in the course of Bartlett's criticism are good and some of his suggestions are worthy of recognition. Furthermore, we agree with him on certain points, especially where he calls attention to exaggerations in the use of some expressions, *i.e., Salherbetum.* But we beg Bartlett to believe us when we assure him that we will not forget the responsibility which, according to him, rests upon us. On the other hand, we are much more concerned with logic than with linguistics and would always, if necessary, sacrifice the purity of the classical languages in the interests of clarity and logic.

We may perhaps be allowed to draw attention here to the first paragraph of the fundamental principles of phytogeographical nomenclature as these are set forth in the Transactions of the Third International Botanical Congress held at Brussels (Flahault and Schröter, '10):

" Nomenclature is an *aid to science,* and is intended to facilitate progress; its function is *essentially and entirely practical.* Those who study one and the same science must try to understand each other. All *pretentions to erudition and pedantry* are useless to science and should be ignored."

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REVIEWS

Ecological Sociology[1]

This ambitious essay has been prepared by a plant ecologist and is an attempt to point out certain relationships between generalized ecological methods of thinking and the present economic and biological position of human society. The article undoubtedly is motivated by the seriousness of contemporary human problems and takes the view that man's progress, both cultural and materialistic, is at a point where radical changes, either for better or for worse, are inevitable. In other words, civilization is 'at the crossroads': it may follow the accessible but degenerate path of emotionalism, the culture-depriving system of gross materialism, or may wisely adopt the 'true spirit of science' with a goal of human betterment and æsthetic concord. Obviously, Professor Phillips is an advocate of the latter course and in this paper analyzes his problem by first presenting a few profound obstacles facing the human progress of today and follows this with suggestions for reconstruction which are emergent from ecological studies and thought.

Phillips points out that at the present time our civilization is changing from a rural or more typical biotic community to an urban or less typical community. In the latter habitat man has become a 'super-dominant' part of his environment. This aggregation into cities while serving many beneficial functions is also developing new problems of sociological nature which must be dealt with. Man's habits seem to be changing along with the new complexity of group living: he seeks more sedentary than active methods of amusement; his nervous system is adversely affected by the innumerable kinds of noise-makers he has produced; much of his travel and handiwork are performed by elaborate machines; modern foods are causing increasing amounts of tooth decay, etc. The results of such effects of overcrowding seem to spell decreased national and individual physical vigor and the evolution of a dreary, hopeless uniformity of outlook.

Truly then man is at the crossroads and in a precarious racial position. What can the ecologist suggest in the way of a program for human betterment? From ecological knowledge of such subjects as cause and effect, community integration, the relation of the whole and its parts, competition and cooperation, optimum association, and cyclic phenomena Professor Phillips draws certain conclusions too lengthy to detail here. Of special interest are the author's deductions based on the cooperation existing among social and sub-social animals. It is his view that human society may profit much by

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[1] **Phillips, John F. V.** 1932. Our changing world-view. Lecture iv. Man at the Crossroads. *University of Witwatersrand, Johannesburg, S. Africa.*

copying such behavior and placing it actively to the front as a corrective measure for many of our social ills. That is he feels that a considerable amount of international misunderstanding could be eliminated by adopting a philosophy of conscious cooperation and ingraining it so thoroughly in our social system that its presence would be taken for granted and its authority supreme.

In conclusion, it may be said, that while this essay does not settle our present human problems it does point out some interesting features which, coupled with the fact that Professor Phillips approaches the situation from an ecological viewpoint, makes the article entirely worthy of our attention.

Thomas Park

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Gorillas in a Native Habitat[1]

Readers of Yerkes and Yerkes, "The Great Apes," will be prepared for the major contribution made by Bingham in the present monograph, which seems to be a demonstration of the slight basis upon which rests much of our so-called information concerning the social customs and habits of gorillas in nature. Coincidentally there appears a definite method which he demonstrates will yield more knowledge of the behavior of this much discussed animal.

For two months the Binghams studied the relations of *Gorilla beringei* in its mountainous habitat in the Parc National Albert. The time was equally divided between the upper edge of the bamboo or tropical forest at an altitude of about 6000 feet and an altitude from about 9000 feet up as high as gorillas were found. Their method was to take up the trail of a band of gorillas and follow them until contact was established. Trail histories covering up to about 100 hours of gorilla activities were studied. From the traces of various sorts left by these slowly traveling groups: nests, excreta, food remnants, tramplings, etc., and by direct observation after contact was established, they were able to occupy their time fully and profitably in their psychobiological studies. The point of view is rigorously objective and it is the steady maintenance of this attitude which demonstrates how much of the reports of others have rested on surmise rather than on direct observation.

It is interesting to note the following facts. The gorillas pass the night in nests which are seldom occupied more than one night and which at times are occupied for only a part of the night since there is evidence that a given band builds more nests than there are individuals. In the lower zone among the bamboos, gorilla nests occur in trees in conjunction with nearby ground nests of like age. The tree nests were occupied, apparently, by the gorillas of intermediate size. The pattern of gorilla nests was sufficiently uniform to enable the observers to differentiate between gorilla and chimpanzee nests

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[1] **Bingham, Harold C.** 1932. Gorillas in a Native Habitat. *Carnegie Inst., Washington, Publ. 426.* 64 pp., 22 pl.

where the two ranges overlapped, but showed a wide adaptation to local conditions.

The social responses of different individuals were by no means stereotyped. They were not uniform within the band nor from one band to another. The groups varied in size; as many as 30 are recorded in one band. There were never more than a few young individuals in a band. The animals do not always move off early in the morning; frequently after leaving their night nests they collect in a fairly compact group about some tree or other marked environmental element.

The monograph abounds with recognized but unsolved problems which are important to the ecologist as well as to the psychobiologist. Among these is the question of the extent of the wandering of a given band; the effect of local weather conditions upon movements; the relations between bands; the relations between the two major habitats and the organization of any given group. Further patient application of the trail-study method should give us much information in these matters.

As one looks at the work as reported, one sees not only the gorillas but the observers as well. This composite picture has its amusing side, for we find these relatively puny human animals, protected, it is true, from the rage of even a charging gorilla by their weapons, hanging on the outskirts of these gorilla bands like some inquisitive monkey about the forest camp of men. It is the virtue of this report that the reader is allowed to feel the difficulties of complete observation and the author's sense of the meagerness of his accomplishments. All this leads us to the conclusion that at last such field studies have been put on a sound basis which should result in the hunting of information rather than of specimens.

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ZOOGEOGRAPHICA, INTERNATIONAL REVIEW FOR COMPARATIVE AND CAUSAL ANIMAL GEOGRAPHY

For a long time articles of special interest to the animal geographer and closely allied subject matter have appeared in a variety of journals. Unlike other wide fields of zoology, Animal Geography has heretofore had no special periodical to cover the vast amount of material written on this subject. In order to fill this gap in the special periodical field the editors of *Zoogeographica* have undertaken its publication.

To date three numbers have appeared. Articles are accepted in English, French and German in accordance with its international character. The editors are endeavoring to secure the best collaborators whose contributions may cast light upon questions of animal geography from various angles, both original articles and collective reports being accepted.

It would seem from a preliminary survey of the first three numbers that the editorial staff is successfully fulfilling this real need in the field of special journals. The magazine is well organized, the articles seem well chosen and the general appearance is attractive. One would expect this unique journal to make a wide appeal to specialists and others interested in the subject of animal geography.

Zoogeographica is to appear at irregular intervals forming a single volume of about 640 pages each year with a price per volume of 45 Marks. Thus far, numbers have appeared in January and July of 1932 and February of 1933. Contributors are paid at the rate of 40 German Marks per sheet of sixteen pages and receive fifty reprints free. Articles are to be sent to the editor.

The editorial duties of the magazine have been assumed by Fridthjof Okland of Oslo assisted by Sven Ekman of Upsala and Richard Hesse of Berlin, and is published by Gustav Fischer in Jena.

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SOIL REACTION AND FOREST TYPES IN THE DUKE FOREST

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An investigation of the soil reaction under seven forest types, and in eight soil types in the Duke Forest was undertaken during the winter of 1931–1932 in order to determine the relation, if any, between the H-ion concentration of the soil and the distribution of the forest types.

Previous Work

A considerable amount of work has been done on the influence of soil reaction on plant distribution. Cain ('31) working in the Great Smoky Mountain National Park of North Carolina and Tennessee found that the surface soil, beneath the duff, averaged 0.2 pH more acid than the soil at six inches from the surface. He found a correlation between soil reaction and altitude, the soil becoming more acid with increasing elevation. From his work in the Great Smoky Mountains, he concluded that the plant associations studied showed wide ranges of tolerance to hydrogen-ion concentration, and that " no two contiguous associations can be separated on a basis of reaction alone because of the considerable extent of over-lapping both of surface and subsoil reactions, although one association may be definitely more acid than another on a basis of averages." He found no concrete evidence of one plant association being replaced by a more acid-tolerant one.

Cain and Friesner ('29) in their study of soil reaction and plant distribution in the Sycamore Creek region of Indiana found a striking correlation between the reaction of both the surface and subsoil and the character of the topography, the acidity increasing with increases in elevation. In most cases they found the subsoil to be more acid than the surface soil, although the surface soil samples were taken immediately beneath the litter " in the soil layer of highest organic content." The beech-maple climax forest was found throughout the range of reaction. Christophersen ('23) in his work on the soil reaction in Sylene National Park, Norway, took samples from the region of greatest root development, which was the raw humus in all podsolized soils. He found that the reaction of the soil of one particular association may vary considerably from place to place, but the association "may be limited to a relatively narrow range of soil reaction, which is characteristic for each association." Kurz ('23) in his work on soil reaction in the Starved Rock State Park, Illinois and in the sand dunes around Lake Michigan observed that acid clays or silts, and acid sands were characterized by decidedly different plant associations. Kelley ('23) working on five soil types in Pennsylvania found a relationship between the productivity of the soils and their reaction. In the Hagerstown loam, a deep limestone soil, which was considered well adapted to crop production, the average reaction was pH 6.9, while in the Conowingo loam, considered "very poor," the reaction was pH 5.4. Monthly tests showed a slight variation in reaction, and periods of drought were usually accompanied by an increase in acidity. Moore ('22) concluded, from his work on the effects of humus and lime on the growth of tree seedlings, that alkalinity is more unfavorable to tree growth than acidity of the same departure from the neutral point. Wherry ('22) observed that red cedar reaches its maximum development in the limestone barrens of Tennessee where the surface soil is minimialkaline (pH 7.0–pH 8.0). He states that "this tree becomes prominent on basic igneous rocks, calcareous clays, and various other substrata in which lime is present in an available form near the surface."

DESCRIPTION OF THE DUKE FOREST

The Duke Forest, consisting of approximately 5000 acres of land in Durham and Orange Counties, North Carolina, is located in the lower Piedmont region. The topography is rolling with elevations ranging from 280 to 650 feet above sea level. The soils vary greatly in physical and chemical composition, and in color, texture, and structure. The forest types studied in this work occur on the following soil types that were mapped by the U. S. Bureau of Soils in the soil surveys of Orange County in 1918 and of Durham County in 1920 as: Whitestore sandy loam, Whitestore fine sandy loam (shallow phase), Iredell loam, Conowingo silt loam, Georgeville gravelly silt loam, Georgeville stony silt loam, Congaree silt loam, and Davidson clay loam. Soils of the Whitestore series are derived from Triassic rocks (sandstone, mudstone, and shale). The Georgeville soils are derived from slate of the Carolina Slate Belt. The Davidson and Iredell soils are derived from dark colored igneous rocks such as diorite and diabase. However, the Iredell soils are much younger than the Davidson soils which are of a lateritic character. The Conowingo soils are derived from medium dark-colored igneous rocks such as serpentine, and talose and chloritic schist. The igneous rocks from which the Davidson, Iredell, and Conowingo soils are derived are believed to have been forced through fissures in the slate and Triassic rocks while in the molten state. The Congaree soils are derived from alluvium.

The work in this study was done in the following forest types: loblolly pine, shortleaf pine, white oak-black oak-red oak, post oak-blackjack oak, red gum-yellow poplar, river birch-sycamore, and red cedar. The loblolly pine type occurs as pure loblolly pine, *Pinus taeda,* on old fields with an understory of red cedar, *Juniperus virginiana,* dogwood, *Cornus florida,* sourwood, *Oxydendrum arboreum,* red maple, *Acer rubrum,* black gum, *Nyssa sylvatica,* and redbud, *Cercis canadensis,* or with loblolly pine predominating and the following species as characteristic associates: shortleaf pine, *P. echinata,* yellow poplar, *Liriodendron tulipifera,* red gum, *Liquidambar styraciflua,* ash, *Fraxinus* spp., elm, *Ulmus* spp., red oak, *Quercus borealis,* scarlet oak, *Q. coccinea,* and white oak, *Q. alba.* The understory is about the same as in the pure type. The shortleaf pine type occurs both as pure shortleaf pine on old fields and as shortleaf pine with the following characteristic associated species: loblolly pine, white oak, scarlet oak, post oak, *Q. stellata,* blackjack oak, *Q. marilandica,* southern red oak, *Q. rubra,* and persimmon *Diospyros virginiana.* The characteristic species of the understory are red cedar, dogwood, and sourwood. In general the shortleaf pine type occurs on drier sites than does the loblolly pine type.

The predominant species of the white oak-black oak-red oak type in the Forest are white oak, red oak, and southern red oak. Black oak, *Q. velutina,* occurs only occasionally. Characteristic associated species in this type are: scarlet oak, post oak, hickory, *Hicoria* spp., ash, black gum, elm, and persimmon. Conspicuous members of the understory in this type are: dogwood, sourwood, ironwood, *Ostrya virginiana,* redbud, and red cedar.

The red gum-yellow poplar type occurs as almost pure red gum and yellow poplar on old bottomland fields, or with the following characteristic associates: loblolly pine, sycamore, *Platanus occidentalis,* river birch, *Betula nigra,* black gum, ash, elm, and red oak. The understory is composed largely of redbud, red cedar, and dogwood. Sycamore usually predominates in the river birch-sycamore type. Associated with it are: river birch, loblolly pine, yellow poplar, red gum, ash, black gum, and elm. Common members of the understory are dogwood, blue beech, *Carpinus caroliniana,* red maple, sourwood, and red cedar. The stands studied in the river birch-sycamore type were pure sycamore. The red cedar type as recognized in this study occurs as very small stands of pure red cedar in the other types. It seldom occurs in the overstory on extensive areas. Soil samples were collected under red cedar trees only where the litter and fermentation layers appeared to be composed largely of red cedar material.

The stands of the red gum-yellow poplar and river birch-sycamore types under which soil samples were taken are all on Congaree silt loam. The loblolly pine stands studied occur on Georgeville gravelly silt loam and Congaree silt loam. All of the shortleaf pine stands studied are on Whitestore sandy loam and Whitestore fine sandy loam, shallow phase. The stands of the white oak-black oak-red oak type are on Davidson clay loam, Georgeville gravelly silt loam, and Georgeville stony silt loam. The stands of the post oak-blackjack oak type are on Georgeville stony silt loam and Iredell loam. The small stands or groups of red cedar are on Georgeville stony silt loam. All of the pure pine and the greater part of the red gum-yellow poplar stands are second growth. The pine came in on old fields that were at one time tilled. The pine stands from which samples were taken are from 30 to 80 years old. Stands of the red gum-yellow poplar type from which samples were taken are from 30 to 70 years old, and some of them are even-aged as a result of clear cutting but there is no evidence that the land has ever been farmed. Stands of the white oak-black oak-red oak type from which samples were taken are uneven-aged, while those in the post oak-blackjack oak type are from 21 to 40 years old. The two oak types occupy virgin soil. The groups of red cedar are second-growth, and occur on both old field and virgin soils.

METHODS AND RESULTS OF PRESENT STUDY

Over five hundred soil samples were taken from ninety profiles in the seven forest types studied. Samples of organic material were obtained from the litter, fermentation, and humus layers. In the mineral soil, samples were taken at three depths from the surface: 0 to 2-inches, 6 to 8-inches, and 16 to 18-inches. Samples taken at the 0 to 2-inch depth were always made up of the A_1 horizon and usually the upper part of the A_2 horizon. The 6 to 8-inch depth usually occurred in the A_2 horizon although the upper part of the B horizon was sometimes encountered at this depth. Samples from the 16 to 18-inch depth were usually in the B horizon, although in the shallower parts of the Georgeville and Whitestore soils the upper part of the C horizon was encountered. A soil auger was used to obtain samples from the two lower depths in the mineral soil. Samples were carried from the field to the laboratory in sixteen ounce tin soil cans or in paper bags. Paper bags were never used for wet soil. About 200 grams of mineral soil were taken for a sample, and approximately 100 grams from the organic layers. Approximately 40 grams of soil were taken from the field sample, after it had been thoroughly mixed, placed in 120 cc. of distilled water and shaken by hand for dispersion. The soil-water solutions were then placed in a cold room kept at 34° to 36° F. and allowed to stand for 24 hours before testing.

The H-ion concentration was measured colorimetrically[1] with a series of indicators and buffer solutions. The following indicators were used to cover the range of reactions: Brom phenol blue, pH range, 3.0–4.6; Brom cresol green, 3.8–5.4; Chlor phenol red, 4.8–6.4; Brom cresol purple, 5.2–6.8; Brom thymol blue, 6.0–7.6; Phenol red, 6.8–8.4; and Cresol red, 7.2–8.8.

Clark and Lubs series of buffer solutions were made up according to Clark ('28, pp. 192–220), to cover the range of reactions from pH 3.0 to pH 8.0 at 0.2 pH unit intervals. The buffer solutions were checked with the quinhydrone electrode before using.

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[1] The writer is indebted to Dr. Paul J. Kramer of the Botany Department of Duke University for the preparation of reagents used in this study.

A porcelain comparator plate with twelve depressions was used for making the tests. Following a few preliminary experiments a ratio of one part of indicator to fifteen parts of the soil-water solution was finally used. The same ratio of indicator to buffer solution was used for the color standard. The H-ion concentration was easily determined to 0.1 pH in all but the turbid solutions. The turbid solutions were diluted from one to two times with distilled water in order to obtain a solution that could be tested accurately. Results of preliminary tests indicated that such dilution does not change the reaction enough to be significant in this type of work. Centrifuging for ten minutes at a speed of 3200 R.P.M. was found to be ineffective in reducing the turbidity of most solutions. The work of Gustafson ('28) shows that filtering changes the reaction of the solutions of some soils.

The results of H-ion concentration measurements from the seven forest types are presented in table I and in figure 1. A rather striking gradient of the reaction of the soils toward alkalinity is apparent under the two pine and two oak types, while in the two bottomland types, red gum-yellow poplar and river birch-sycamore, this gradient is less pronounced. Under groups of red cedar there is a slight gradient towards alkalinity from litter to the humus layer, but from the humus layer on through the first eighteen inches of mineral soil there is a gradient towards acidity. The fermentation layers were less acid than the litter in all forest types except loblolly pine and in all types the humus layers were less acid than the fermentation layers. In all types except red gum-yellow poplar and red cedar the surface-soil layers were less acid than the humus layers.

As is brought out in table I and in figure 1 the three organic layers have characteristic average reactions. These data show that the decomposition of organic materials above the surface of the mineral soil is accompanied by a decrease in its acidity. The reactions of the different organic layers undoubtedly are an important factor in determining the kind of microorganisms that will develop and continue the decomposition process. At the same time the organisms at work in the organic material may produce certain characteristic reactions in their growing media. One would expect to find a somewhat different group of organisms working in the different organic layers under red cedar as compared to the pine types.

The importance of the reaction of the organic material in the development of a podsol profile has been brought out by numerous investigators. Fisher ('28) found a characteristic podsol profile in the Harvard Forest in central Massachusetts under an 80-year old stand of white pine, while in an adjacent stand of 18-year old hardwoods a mull profile was evident, although the soil exhibited a podsol profile at the time the pine was removed and the hardwoods allowed to come in. In the Duke Forest humus weathering of the A_2 horizon (leached layer) is probably going on more rapidly in the pine types than in the types that produce a litter of relatively low H-ion concentration as in the red gum-yellow poplar and river birch-sycamore types. However, podsoliza-

TABLE I. *Soil reaction by forest type and profile region*

Profile region	Number of samples	Average reaction		Range of reaction in pH units
		pH units	Active[1] acidity	
Loblolly pine type				
Litter	18	4.2	630	3.8–4.8
Fermentation	18	4.2	630	3.8–5.1
Humus	17	4.7	200	4.2–5.9
0 to 2 inches	17	6.0	10	5.4–6.5
6 to 8 inches	18	5.8	16	5.7–6.5
16 to 18 inches	17	6.1	8	5.9–7.0
Shortleaf pine type				
Litter	20	4.3	500	3.7–4.7
Fermentation	16	4.7	200	4.4–5.5
Humus	14	5.2	63	4.8–6.1
0 to 2 inches	20	6.0	10	5.6–6.5
6 to 8 inches	20	5.8	16	5.5–6.3
16 to 18 inches	20	5.8	16	5.5–6.5
White oak-Black oak-Red oak type				
Litter	10	4.1	790	3.8–4.7
Fermentation	11	4.9	125	4.5–6.2
Humus	11	5.4	40	5.0–6.2
0 to 2 inches	10	5.9	12.5	5.4–6.3
6 to 8 inches	11	6.1	8	5.7–6.5
16 to 18 inches	9	6.4	4	6.0–7.0
Post oak-Blackjack oak type				
Litter	12	4.1	790	3.7–4.4
Fermentation	12	4.5	315	4.3–4.8
Humus	11	5.8	16	5.2–6.4
0 to 2 inches	12	6.1	8	5.9–6.4
6 to 8 inches	12	6.0	10	5.8–6.4
16 to 18 inches	12	6.0	10	5.9–6.4
Red gum-Yellow poplar type				
Litter	12	4.6	250	4.2–5.4
Fermentation	11	5.9	12.5	5.7–6.3
Humus	1	6.3	5	6.3
0 to 2 inches	13	6.3	5	6.0–6.9
6 to 8 inches	13	6.0	10	5.7–6.4
16 to 18 inches	12	6.1	8	5.7–6.9
River birch-Sycamore type[2]				
Litter	4	5.8	16	5.7–5.8
Fermentation	4	6.1	8	6.0–6.2
Humus	—	—	—	—
0 to 2 inches	4	6.1	8	6.0–6.2
6 to 8 inches	4	6.0	10	6.0
16 to 18 inches	4	6.1	8	6.0–6.2
Red cedar type[3]				
Litter	9	6.4	4	6.1–6.9
Fermentation	8	6.9	0.5	6.4–7.3
Humus	2	7.0	0	6.9–7.3
0 to 2 inches	9	6.7	1.5	6.4–7.4
6 to 8 inches	8	6.2	6	5.9–6.6
16 to 18 inches	8	6.3	5	6.1–6.6

[1] After Wherry ('27).

[2] Pure sycamore.

[3] Not a recognized type in the Forest. Samples taken under groups or clumps of trees.

tion is undoubtedly very slow in this section of the continent because of the generally temperate climate with mild winters during which organic decomposition is arrested but little.

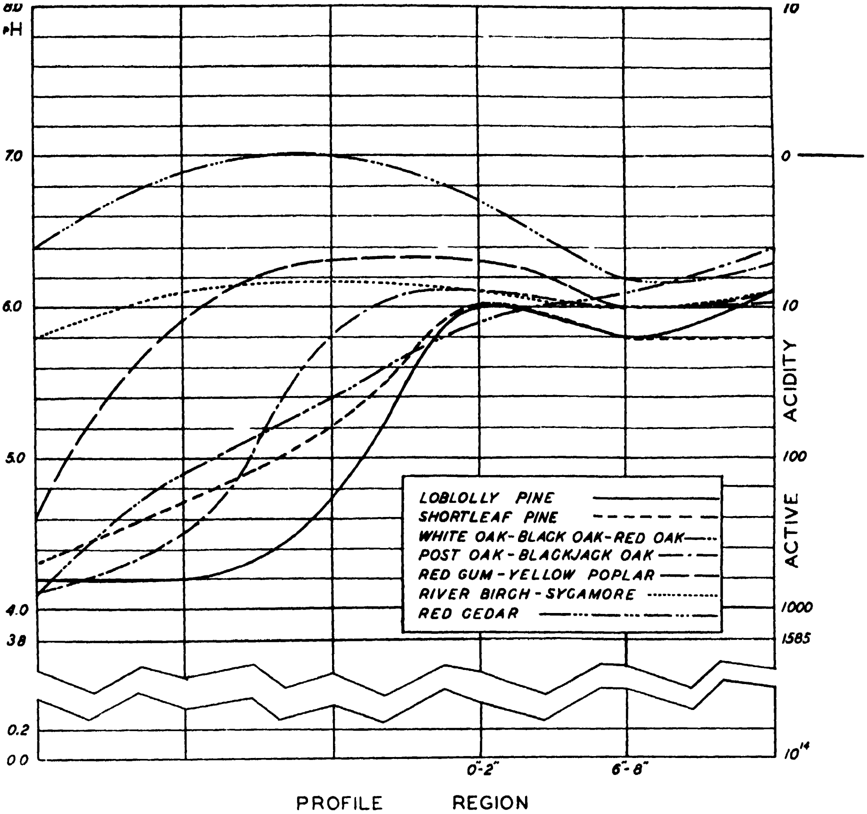

FIG. 1. Soil reaction curves for seven forest types. The three layers of the organic material are designated: L = litter, F = fermentation, and H = humus. 0 to 2-inches, 6 to 8-inches, and 16 to 18-inches refer to depths from the surface. Reaction in pH units is given on the left vertical axis and reaction in terms of "active acidity" is given on the right vertical axis.

Differences in the reaction of the mineral soil under the seven forest types as measured colorimetrically are very small and are probably an unimportant factor in the distribution of the forest types. These differences have still less significance when we consider that the different soil types may show as great or greater differences in reaction under a given forest cover or in open fields. However, the reaction of the organic layers under loblolly and shortleaf pines, may be a limiting factor in the establishment of the seedlings of certain species whose organic material is much less acid, as the characteristic. species of the red gum-yellow poplar and river birch-sycamore types.

The surface soil under groups of red cedar shows the effect of the incorporation of nearly neutral humus. The average reaction of nine samples of the surface soil under red cedar was pH 6.7 as compared to an average reaction of about pH 6.0 for all other types. It would appear from this that red cedar tends to make its soil more alkaline when it is on acid soils. Red cedar occurs as scattered trees in the understory throughout the Forest in all forest types and on all soil types. Where the humus layer is made up entirely of decomposed red cedar litter it does not lie upon the surface of the mineral soil as a distinct layer, but the two are so intermixed that no sharp line of demarcation is evident in most cases. The almost neutral reaction of the organic material under red cedar may result in increased activity of certain organisms thereby bringing about a rapid mixing of the humus with the mineral soil. Several species of mosses and lichens are found on the poor sites supporting red cedar, but they are not found directly under the trees as may be the case in the post oak-blackjack oak type on poor sites. A fairly dense ground cover of violet, *Viola sororia,* is often found directly under the cedar, while few plants of this species are found under adjacent pines and hardwoods. The absence of vegetation, other than violets, under dense groups of red cedar is probably associated with the insufficient moisture and possibly with insufficient light, rather than the almost neutral reaction of the organic soil.

The average reaction of the surface soil in the red gum-yellow poplar type was about 0.3 pH less acid than the surface soils under the other types, with the exception of red cedar. This, also, brings out the effect of the incorporation of less acid humus into the surface mineral soil under the red gum-yellow poplar type on its reaction as compared with the pine types and the other hardwood types. A distinct humus layer was not often found in the red gum-yellow poplar type on alluvial soil. In this type there appears to be a rapid breaking down and incorporation of the organic material into the mineral soil. The incorporation of this rapidly decomposing organic residue is so complete that the A_1 horizon is not as distinct as it is under other forest types which produce litter that is more acid and is decomposed and incorporated into the surface mineral soil less rapidly. The river birch-sycamore type appears to be quite like the red gum-yellow poplar type with regard to the relatively rapid breaking down and incorporation of organic material into the mineral soil. The frequent rise and fall of the water table and the physical properties of the bottomland soil are probably important factors in the failure of humus material to be collected in a distinct A_1 horizon.

The post oak-blackjack oak type is found on what appears to be the poorest sites in the Forest. In this type only about one-half of the forest floor is covered with litter, the remaining half is occupied largely by mosses and lichens.[2] The most conspicuous mosses are: *Dicranum scoparium, Anomodon attenuatus, Thuidium delicatulum,* and *Cirriphyllum boscii. Cladonia sylvatica* and *C. pyxidata* are common lichens found on this site.

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[2] The writer is indebted to Dr. Hugo L. Blomquist of the Botany Department of Duke University for identifying the mosses and lichens.

TABLE II. *Effect of storage in paper bags for a period of 4 months on soil reaction*

	0 to 2-inches			6 to 8-inches			16 to 18-inches		
	Number of samples	Average reaction	Range	Number of samples	Average reaction	Range	Number of samples	Average reaction	Range
Fresh	11	5.9	5.6–6.4	12	5.9	5.6–6.4	5	6.2	5.9–6.6
Stored	11	5.9	5.6–6.4	12	6.1	5.9–6.5	5	6.2	6.0–6.4

TABLE III. *Comparison of the results of soil reaction tests made colorimetrically and with the quinhydrone electrode*

Method	Litter			Fermentation			Humus			0 to 2-inches			6 to 8-inches			16 to 18-inches		
	No. of samples	Average reaction in pH units	Range	No. of samples	Average reaction in pH units	Range	No. of samples	Average reaction in pH units	Range	No. of samples	Average reaction in pH units	Range	No. of samples	Average reaction in pH units	Range	No. of samples	Average reaction in pH units	Range
Colorimetric	9	4.5	4.3–4.8	8	4.7	4.3–5.5	7	5.4	5.1–5.9	31	6.0	5.4–6.5	27	6.1	5.8–6.5	19	6.2	5.8–7.0
Quinhydrone	9	4.3	4.2–4.5	8	4.5	4.0–4.9	7	4.9	4.7–5.4	31	5.2	4.7–5.8	27	5.3	5.0–5.8	19	5.6	5.3–5.8

A few samples of the mineral soil, disregarding soil types and forest types, were stored in paper bags in the laboratory for a period of 4 months. The results of H-ion concentration determinations before and after storage are presented in table II. The data for the soils tested colorimetrically show that there is little, if any, change in the reaction of the mineral soil due to air drying and storage in paper bags. These few data substantiate the results obtained by Gustafson ('28). However, there may be a slight change in reaction toward alkalinity as is evident in the 6 to 8-inch depth, but this slight change is not made apparent in averaging the logarithmic equivalents of reactions between pH 5.8 and pH 6.8 because of the logarithmic decrease in H-ion concentration toward neutrality as expressed in pH units. An exhaustive study by Bailey ('32) shows that a great many soils become slightly more acid after being air-dried and stored.

A comparison of tests made colorimetrically, and electrometrically with the quinhydrone electrode and a calomel half-cell are presented in table III. Samples of the litter, fermentation, and humus layers were taken from the loblolly pine and shortleaf pine types, but the samples from the mineral soil were taken at random from all forest types and soil types; this procedure was considered justifiable since the reaction of the mineral soil under different forest types and in different soil types did not seem to vary greatly, as determined colorimetrically under the conditions of the experiment. For all six regions of the profile the quinhydrone electrode gave more acid reactions than the colorimetric method. The closest agreement between the two methods was found in the litter and fermentation layers, the average reaction for samples tested with the quinhydrone electrode being only 0.2 pH unit lower than the colorimetric method. The greatest divergence was in the two upper regions of the mineral soil where the average reaction as determined with the quinhydrone electrode was 0.8 pH unit lower than the average reaction as determined colorimetrically.

Evidence that the quinhydrone electrode method is unreliable for neutral or alkaline material was brought out in testing a sample from the red cedar fermentation layer. The reaction immediately after the quinhydrone was placed in the solution was pH 6.5 and ten minutes later it was pH 7.3. The colorimetric method gave a reaction of pH 6.3 for the same sample.

SUMMARY

H-ion concentration determinations were made colorimetrically on over 500 soil samples from the Duke Forest. Ordinarily three samples were taken from the organic soil layers and three samples from the mineral soil from each of ninety profiles distributed under seven forest types and in eight soil types. The organic material, lying upon the mineral soil, was divided into three layers based on extent of decomposition. These three layers (litter, fermentation, and humus) gave characteristically different average reactions. Litter of low

H-ion concentration appears to be decomposed more rapidly and the decomposition products incorporated more rapidly into the mineral soil than litter of relatively high H-ion concentration. Some examples of litter of low H-ion concentration are: red gum, yellow poplar, red maple, river birch, sycamore, and dogwood. Litter of loblolly pine, shortleaf pine, and the oaks has a relatively high H-ion concentration. Red cedar tends to make the surface soil more alkaline, if the surface soil without a cover of red cedar is ordinarily acid.

The soil reactions under seven forest types in the Duke Forest, as determined colorimetrically, do not differ greatly enough to be a limiting factor in the distribution of the forest types.

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A METHOD OF MARKING LIVING SNAKES FOR FUTURE RECOGNITION, WITH A DISCUSSION OF SOME PROBLEMS AND RESULTS[1]

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Several years ago, during certain studies on the habits of snakes, it was realized that some simple system for recognizing individuals must be devised. In working with ring-neck snakes, *Diadophis punctatus edwardsii,* complete scale counts and measurements had been made, the snakes had then been released, and collecting had been done in subsequent years in the vicinity of release. It was found, however, that identical scutellation alone was insufficient to establish identity when snakes were recaptured. Later, individual peculiarities were recorded, as well as the scale counts, so that the identity of " returns " could be absolutely established. But to carry out the work on an extensive scale by this method is too laborious, involving, as it does, a complete counting of the scales each time that the snake must be identified. Yet, only by conducting the work on a somewhat extensive scale could sufficient data be obtained for satisfactory conclusions on the problems involved.

One of the studies in which was felt the need of marks for identification was on the rate of growth of snakes under natural conditions. This led to questions on the rate of growth at different times of the year, of the relation of age to size, and of the length of life of the individual and the usual length of life in the species. Another study for which identification of individuals was necessary was that of the home range of an individual snake, or the extent of its wanderings. Closely connected with this is the question of the effect of transporting a snake from its " home range " to a distant point. The possibility, or even probability, of determining something about the snake population of a region was also realized. These questions and others may be successfully investigated if there is available a suitable system of marking individuals.

Marks are necessary wherever it is desired to keep several or many snakes in the same enclosure, and yet to be able to recognize individuals quickly, as is the case in breeding studies which the senior author is conducting at Ann Arbor, Michigan.

METHOD OF MARKING

The method of marking devised consists in snipping a piece from a caudal scute and recording the number of the scale thus marked (figs. 1 to 4).

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[1] Contribution from the Biological Station and the Zoological Laboratory of the University of Michigan.

FIG. 1. Tail of a water snake (*Natrix rhombifera*) with points of scissors in first position for marking a caudal scale.

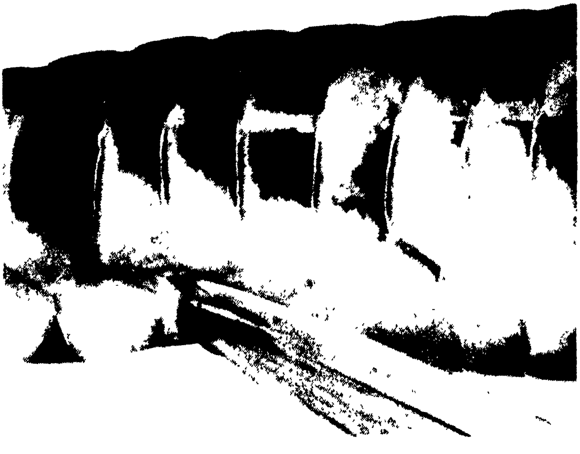

FIG. 2. Same as last, but with points of scissors making the first incision.

FIG. 3. Second position of scissors, with scale nearly cut off, ready to make the final cut.

FIG. 4. The scale has been removed, leaving a large v-shaped cut on the sixth left caudal scute.

Healing leaves a permanent scar (figs. 5 and 6). If only a small portion of the scute is removed the scale regenerates almost completely. But even after such healing, careful observation will show that the scale was marked.

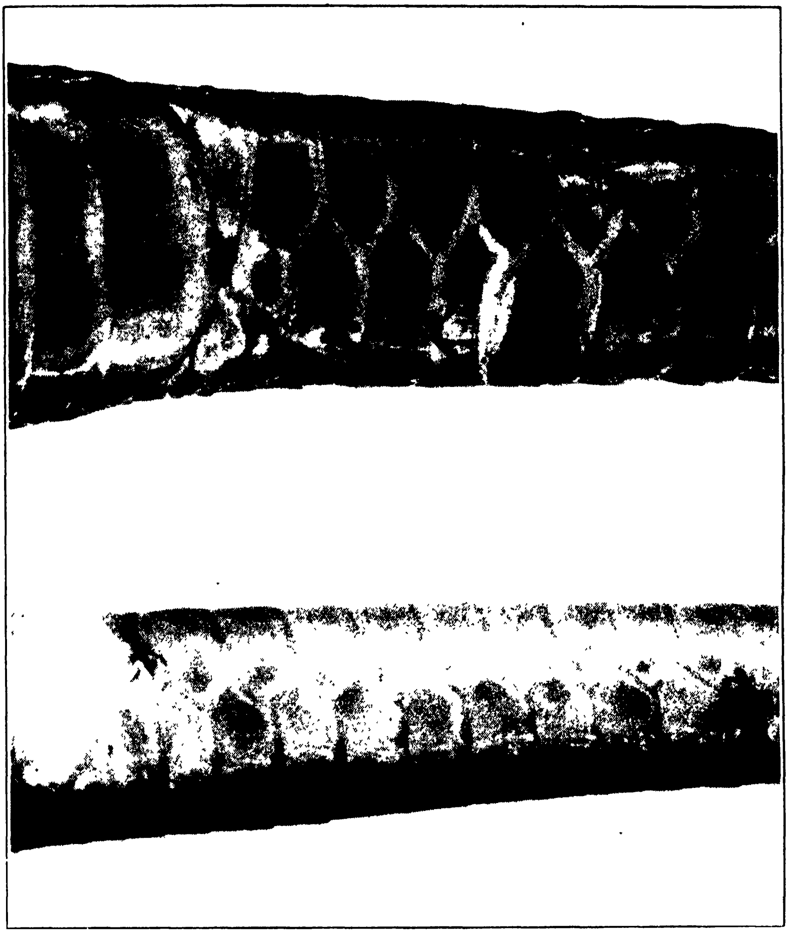

FIG. 5. Tails of two garter snakes (*Thamnophis sirtalis*) showing scars on some of the caudal scutes. Upper figure shows one fresh mark and two scars five months old. Lower figure shows two scars five months old, marking the snake "2–12."

Its posterior edge will be irregular, or more or less of the scale will be discolored. To make the scar really permanent, nearly the whole scale must be removed. This is easily done with a pair of sharp-pointed scissors suited in size to the size of the snake (figs. 1 to 4). The integument must be cut off down to the muscle layer (fig. 4). It seems to be harmless and practically painless to the snake, and for the most part the operation does not even draw blood.

In the system of marking developed, the caudal scutes, *i.e.*, those on the underside of the tail, are counted from the anterior end of the tail. Thus, if the second and fifth left and fourth right caudals are scarred, the snake is designated 2, 5–4. To prevent any error due to uncertainty as to which scale is counted as the first (as there is sometimes a diminutive scale just behind the anus), the most anterior caudal to be marked on either side is always an even number. Usually three scales are marked on each snake, but not more than three, and none are scarred beyond the 20th. This allows ease of identification with an ample series of numbers.

The series of marks in use is as follows:

0–2
0–2, 3
0–2, 3, 4
0–2, 3, 5
0–2, 3, 6
0–2, 3, 7
0–2, 3, 8
to
0–2, 3, 20
0–2, 4
0–2, 4, 5
0–2, 4, 6
0–2, 4, 7
0–2, 4, 8
to
0–2, 4, 20
0–2, 5
0–2, 5, 6
to
0–2, 5, 20

etc. to
0–2, 19, 20
0–2, 20
0–4
0–4, 5
0–4, 5, 6
0–4, 5, 7
0–4, 5, 8
to
0–4, 5, 20
0–4, 6
0–4, 6, 7
to
0–4, 6, 20
etc. to
0–4, 19, 20
etc. to
0–18, 19, 20
0–18, 20
0–20

2–2
2–2, 3
2–2, 4
2–2, 5
to
2–2, 20
2–4
2–4, 5
2–4, 6
to
2–4, 20
etc. to
2–20
4–2
4–2, 3
etc. to
4–20
etc. to
20–18, 20
20–20

2, 3–2
2, 4–2
2, 5–2
to
2, 20–2
2, 3–4
2, 4–4
to
2, 20–4
etc. to
2, 20–20
etc. to
18, 20–20
2, 3–0
2, 3, 4–0
2, 3, 5–0
etc. to
18, 19, 20–0
18, 20–0
20–0

Releases and Recoveries

This work was begun in a small way at the University of Michigan Biological Station in Cheboygan County in the summer of 1929 and has been pursued with increasing vigor in each succeeding summer. The first season's activities resulted in the marking and release of 50 garter snakes (*Thamnophis sirtalis sirtalis*), 3 ribbon snakes (*T. sauritus sauritus*), 13 water snakes (*Natrix sipedon sipedon*) and 3 milk snakes (*Lampropeltis triangulum triangulum*). In 1930 these numbers were materially increased, and in addition 18 red-bellied snakes (*Storeria occipito-maculata*), 61 newly born garter and ribbon snakes and 27 little milk snakes were marked and released. All new-born snakes of a season were given the same mark. Very small snakes can be successfully marked by the method here described, but it is a more tedious operation with them, and on this account and because of the small chance of finding any of them in another year, it was not considered worth while to give them individual marks. When any are caught again, individual numbers are given to replace the group number. From returns of these small snakes it is hoped to accumulate data on rate of growth in early life, the length of the subadult period, and the probable age of the smaller snakes

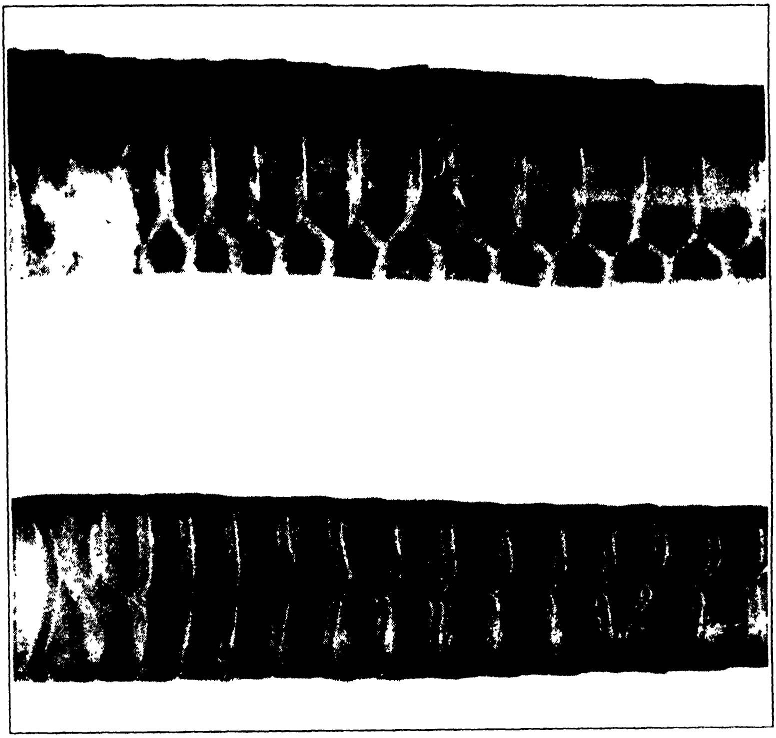

FIG. 6. Tails of two garter snakes each showing one scar two years old.

TABLE I. *Species of snakes and numbers of specimens marked and released from 1929 to 1932. Where two numbers, joined by a plus sign, are given, the first refers to field-collected specimens, the second to new-born young*

Species	1929	1930	1931	1932	Totals
Thamnophis sirtalis	50	65 + 50	142 + 141	169 + 234	426 + 425
T. sauritus	3	9 + 11	19 + 13	35 + 30	66 + 54
Natrix sipedon	13	23	41 + 113	97 + 485	174 + 598
Lampropeltis triangulum ...	3	7 + 28	5 + 13	30 + 0	45 + 41
Storeria occipito-maculata ..		22	7 + 44	15 + 39	44 + 83
S. dekayi				2 + 12	2 + 12
Liopeltis vernalis	3	11 + 75	14 + 51	26 + 30	54 + 156
Totals	72	137 + 164	228 + 375	374 + 830	811 + 1369

collected in the field. In 1931 the number of new snakes marked and released was nearly double that of the two previous seasons together, and the number released in 1932 was much greater than in 1931. These details are summarized in table I. Work of this sort gathers momentum as it progresses.

Without assistance each summer from the Faculty Research Fund of the University of Michigan it would have been quite impossible to carry out this work on a scale commensurate with its promise of results.

The supply of snakes has been obtained mostly from special snake-hunting trips to many places in Cheboygan and Emmet Counties, but many specimens have been found by chance and donated by members of the Station who are kindly disposed toward the work. Beginning with August, 1929, all releases have been on Douglas Lake (with the exception of the ring-neck snakes). *Natrix* and species of *Thamnophis* have been liberated at certain places along the shore of Douglas Lake, on which the Michigan Biological Station is located. Although some have been released near the Station, most of them have been put at places where there are beach pools or swamps abounding with frogs and tadpoles of *Rana pipiens* and *R. clamitans,* and where also the newt *Triturus viridescens* and several species of fish are plentiful. Old logs and stumps provide shelter. These places are known locally as Sedge Point, Deer Point, Hook Point, and East Point (fig. 7). The terrestrial species

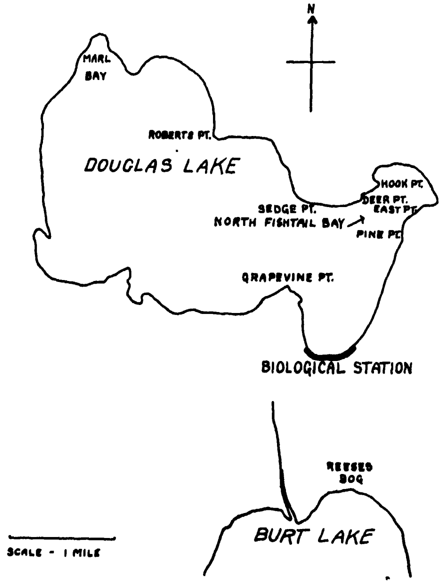

FIG. 7. Outline map of Douglas Lake showing places referred to in the text.

have been released in the vicinity of the Station, either just outside the door of Vertebrate Laboratory, or near one of the faculty houses, or at the east or west end of the Station grounds. In a good many instances, of course, care has been taken to release snakes at the exact places where they were captured.

Recoveries of snakes released in a previous season (exclusive of new-born young) have amounted to 6.3 per cent of the garter snakes, 6.5 per cent of the ribbon snakes and 7.8 per cent of the water snakes. If recoveries of these semi-aquatic species are maintained at something like these rates, the data obtained will well justify the labor involved. So far none of the terrestrial snakes have been recovered later than the same season. The actual numbers recovered and the species represented are shown in table II.

As examples of some of the possibilities of this type of work a few of the preliminary results are summarized below. All reference, however, to the work on ring-neck snakes (*Diadophis punctatus edwardsii*) is omitted from this account in favor of a separate presentation at a future date. Aside from this species, the best results so far have come from the garter snakes and the water snakes. This is because they are relatively abundant in the region and their habitat preferences make it easier to find them. The more terrestrial species are much more difficult to obtain in numbers for release and are harder to find again afterwards. From some of them, however, interesting bits of information have already been obtained.

WANDERINGS

The wanderings of snakes, as indicated by recaptures, give little chance as yet for generalization, but they are interesting in their diversity. In 1931, 19 snakes of four species were recaptured after intervals of from one hour to one month. One garter snake, after an hour, was found 1800 feet from its starting place. Another, after one month, was found only 540 feet away. The second was liberated where found, the first at a different place. Only one released during the previous year was recovered; during 11 months and

TABLE II. *Species of snakes and numbers of specimens recovered after marking and release. In the last column where a plus sign is used the left figure refers to field-collected specimens of all sizes, the right to young of the previous year*

	Recoveries in same season			
	1930	1931	1932	
Thamnophis sirtalis	5	12	8	
T. sauritus		2	4	
Natrix sipedon		2	16	
Lampropeltis triangulum			7	
Storeria occipito-maculata		3[1]		
Liopeltis vernalis			1	
Totals	5	19	36	
	Recoveries from a previous season			
	1930	1931	1932	Percentage recovered in 1932
T. sirtalis		1	14 + 1	6.3 + 0.7
T. sauritus			2	6.5
N. sipedon			6 + 4	7.8 + 3.5

[1] Same individual recovered three times.

18 days it had covered a distance of a mile and a half along the lake shore (Deer Point to East Point, fig. 7). An adult male *Natrix* traveled a mile and a half along the beach in three weeks (from Sedge Point to Roberts Point). It was killed by a summer vacationist who found it with a perch in its mouth. In 1932 an adult female *Natrix* wandered three and a half miles along shore (from the Station Boat House to Hook Point) during only six days in midsummer. There is of course the possibility of some of this route being taken by swimming in the lake. The wanderings of most of the "returns" of this species (*Natrix sipedon*) were limited to short distance up to half a mile.

In 1932, 15 garter snakes (including one born the previous year), 2 ribbon snakes and 10 water snakes (including four born in captivity the summer before) were recovered from those released in previous years. Of three garter snakes released in the same place (Sedge Point) at the same time in 1929 (August 12), two were found three years later in the region of release, while one had wandered a distance of at least five miles in the three years. The original sources of these three snakes were not recorded.

Three large female garter snakes released at Deer Point in August 1930 were recovered two years later. One of these was found at Sedge Point, not far away, while the others had traveled at least four miles each, in opposite directions. One was found at Marl Bay, the other at the Station Boat House. The sources of these three snakes had not been recorded.

Nine of the garter snakes released in 1931 and recovered in 1932 are recorded in the last twelve lines of table III. Two placed at Hook Point were recovered in the same vicinity. One released at the laboratory was recovered at North Fishtail Bay, about three miles away. Two released at different points on the Station grounds traveled at least a mile and a half to two miles over rough aspen country to Reeses Bog on Burt Lake. Another released at the Station was found nearby a year later. For none of these snakes was the place of original capture recorded.

One of the snakes that had traveled to Reeses Bog was released at the Station and found nearby six days later. A snake born in the laboratory in 1931 was released in the middle of August and found nearby a year later. Three other snakes found on the Station grounds and released at the points of recovery were found not far away after intervals of 16 days, about 10 months and 11 months.

If in the above records there is a suggestion that a snake wanders little when released where found, a definite instance to the contrary should be noted. An adult male found at Pine Point early in the summer of 1932 was measured and released there on the same day. Forty-four days later it was recovered on the Station grounds at least a mile and a half away.

It is of course likely that more of the garter snakes than noted above traveled away from the shores of Douglas Lake. The chance of recovering such individuals is poor, for although garter snakes are occasionally found

TABLE III. *Wanderings of Thamnophis sirtalis*

Number of snake	Sex	Length in mm. when released	Source	Locality of release	Interval before recovery	Length in mm. when recovered	Locality of recovery	Minimum distance traveled
307	♂	476	Not recorded	Vert. Lab.	1 hour		Log Lab.	1800 feet
166	♂	647	Club House	Club House	1 month		Boat house	540 feet
55	♀	530	Not recorded	Deer Pt.	11 1/2 mos.	685	East Pt.	1 1/2 miles
22	♂	550	" "	Sedge Pt.	2 yrs. 11 mos.	638	Reeses Bog	5 miles
40	♀	600	" "	" "	2 yrs. 11 mos.	643	Same place	None
45	♀	745	" "	" "	2 yrs. 10 2/3 mos.	852	Same place	None
54	♀	655	" "	Deer Pt.	2 yrs.	670	Same region	Little
58	♀	770	" "	" "	2 yrs.	805	Marl Bay	4 miles
109	♀	685	" "	" "	1 yr. 10 mos.	800	Boat house	4 miles
188	♂	594 +	" "	Hook Pt.	1 yr. 1 mo.	626 +	Same region	Little
229	♂	702	" "	" "	11 1/2 mos.	706	Same place	None
262	♀	735	" "	E. end Sta.	10 1/2 mos.	750	Reeses Bog	1 1/2 miles
262	♀	750	Reeses Bog	Vert. Lab.	6 days	758	Station	Little
274	♀	192 ±	Born in Lab.	Station	1 yr.	247	Station	Little
311	♂	435	Not recorded	Vert. Lab.	11 mos.	571	N. F. Bay	3 ± miles
315	♀	745	" "	" "	10 1/2 mos.	758	Reeses Bog	1 1/2 miles
318	♂	625	" "	E. end Sta.	10 mos.	634	Station	Little
347	♂	632	22 State St.	Vert. Lab.	9 2/3 mos.	641	Fac. h. 44	Little
347	♂	641	Fac. h. 44	Fac. h. 44	1/3 mo.	647	Log Lab.	"
449	♀	493	Station	Vert. Lab.	11 mos.	571	Station	"
464	♂	582	Pine Pt.	Pine Pt.	44 days	633	"	1 1/2 miles

in upland situations at a distance from water, their scarcity in such places makes it unprofitable to hunt them there. The wanderings of garter snakes here described are summarized in table III.

Two returns of ribbon snakes are of sufficient interest for record. A female released at Sedge Point, Douglas Lake, August 21, 1930, was recovered at the Biological Station, 4 miles distant along the shore nearly two years later (June 28, 1932). It was then released at the Station and recovered nearby after three weeks and again after eleven more days. Although it bore no young in 1932 and was by no means a large snake for its species (654 mm.), it showed no increase in length in the two years. Its original source is not recorded but it was probably not Sedge Point, where it was set free. Contrast this with another female ribbon snake that was recovered on July 31, 1932, after having been free exactly a year. This snake was released at the place where it was found (Hook Point), and on the same day. It was recovered at the same place a year later. During the year it increased in length from 371 to 477 millimeters.

RATE OF GROWTH

Some preliminary data on rate of growth are interesting. To make the results comparable, the rate has been determined per month, with an allowance of five growing months to the year (May through September). Although in northern Michigan snakes may be seen on occasion in October and April, there is evidence that little, if any, feeding and growth take place in these months. The percentage increase in length each month is obtained by dividing the increase in millimeters by the length of the snake at the beginning of the period and then dividing by the number of months. This percentage has been obtained for the total length and for the body length, but there are more figures for the latter because the tails of several "returns" have suffered shortening during the interval at large. The figures for body length may, however, be used to represent the rate for the total length, at least for adult snakes, because there is very little difference between the two. The rate of increase in length in adult garter snakes averaged about one per cent a month in thirteen specimens, with a variation from 0.17 per cent to 3.3 per cent (table IV). Causes of this variation may be sought in the different favorabilities of different seasons and parts of seasons, in the particular habitat an individual lives in, in the age of the snake, perhaps in the parasites it harbors, and in other factors. It will be noted that the slowest rate of growth was registered by a large male, and the fastest rate by one of the smallest females. The possible influence of the season is suggested by some cases. The years immediately preceding 1932 were unfavorably dry, while 1932 was warm in June, a normally cold month, and favorably wet.

Returns of three sexually immature individuals indicate a much faster growth for that period of life, a rate of 6 to 8 per cent a month.

These rates of growth in garter snakes may be compared with figures

TABLE IV. *Rate of growth in garter snakes, Thamnophis sirtalis*

No.	Sex	Measurements		Date of		Elapsed time in growing months	Length increase in mm.		Rate of increase per growing month			
									Millimeters		Per cent	
		Total	Body	Release	Recovery		Total	Body	Total	Body	Total	Body
274	♀	192 ±		Aug. 16, 1931	Aug. 15, 1932	5	55		11		5.7	
311	♂	435	319	" 18, "	July 14, "	4	136	109	34	27	7.8	8.4
449	♀	493	373	June 11, 1932	" 25, "	1 1/2	42	40	28	27	5.7	7.2
40	♀	600	460	Aug. 12, 1929	" 7, "	14	43	67		4.8		1.0
55	♀		504	" 7, 1930	" 25, 1931	4 1/2		90		16.7		3.3
109	♀	685	535	" 21, "	June 18, 1932	8	115	90	14.4	11.3	2.1	2.1
262	♀	735	577	" 16, 1931	July 2, "	3 1/2	15	18		5.1		.9
315	♀	745	593	" 18, "	June 29, "	3 1/2	13	8	3.9	2.4	.5	.4
45	♀	745	595	" 12, 1929	July 1, "	13 2/3	107	92	7.8	6.7	1.0	1.1
58	♀	770	605	" 7, 1930	Aug. 13, "	10	35	27	3.5	2.7	.5	.4
54	♀		615	" 7, "	" 8, "	10		20		2.0		.3
22	♂	550	445	" 12, 1929	July 9, "	14	88	43	6.3	3.1	1.1	0.7
188	♂	594 +	452	July 11, 1932	Aug. 8, "	6	32	42		7		1.5
318	♂	625	474	Aug. 18, 1931	June 11, "	2 3/4	9	5	3.3	1.8	.5	.4
166	♂	635	483	June 28, "	July 28, 1931	1	12		12.		1.9	
347	♂	641	485	" 11, 1932	June 29, 1932	1/2		6		10		2.0
229	♂	702	539	July 25, 1931	July 8, "	4 1/2	4	4	.9	.9	.13	.17

TABLE V. *Rate of growth in water snakes, Natrix sipedon*

No.	Sex	Measurements		Date of		Elapsed time in growing months	Length increase in mm.		Rate of increase per growing month			
									Millimeters		Per cent	
		Total	Body	Release	Recovery		Total	Body	Total	Body	Total	Body
0–2, 3, 5	♀	252	200	Sept. 15, 1931	July 1, 1932	2 1/2	35 ±		14		6.5[2]	
0–2, 3, 4	♀	253	200	"	"	2 1/2	35 ±		14		6.5[2]	
0–2, 3	♀	306	233	"	"	2 1/2	90 ±		36		16.7[2]	
0–2, 4, 15	♀	308	266	"	July 25, 1932	3 1/2	123 ±		35		11.1[2]	
0–2, 3, 4	♀	253	200	July 2, 1932	" 19, "	1/2	13		26		10.3	
0–6	♀	359	279	Aug. 19, 1931	" 6, "	3 1/2	48		13.7		3.8	
0–6	♀	407		July 6, 1932	" 19, "	6 days	8		40		9.8	
0–2, 4, 13	♀	370	286	" 21, "	Aug. 9, "	19 "	15		22		5.9	
5, 9–0	♂	382	291	Aug. 10, 1930	July 8, "	9 1/3	270	208	54	42	14.1	14.4
0–14	♂	673	525	" 19, 1931	Aug. 13, "	4 3/4	112		24		3.6	
3–3, 8	♀	727	558	July 11, "	July 13, "	5	150	114	30	23	4.1	4.1
0–2, 3, 11	♀	777	587	" 4, 1932	" 16, "	12 days	16		40		5.1	
0–2, 4, 17	♀	811	631	" 27, "	Aug. 14, "	18 "	9		15		1.9	
109	♀	870	685	Oct. 1 ±, 1931	July 19, "	2 2/3	103	84	38	31	4.4	4.6
3–4	♀	1035	833	July 7, "	" 7, "	5	47	47	9.4	9.4	.9	1.1

[2] For these four yearlings, 1932 measurements are given, and growth is computed on a basis of 215 mm., which is the average birth length for a large series of young from this region. The average of these four, a more usable figure, is 10.2.

from a similar number of water snakes, *Natrix sipedon* (table V). The average rate of increase per growing month in six adults is 3.3 per cent, with a variation from 0.9 to 5.1 per cent. The lowest rate was registered by the single very large individual. The average increase of four snakes recaptured during their second summer of life was 10.2 per cent a month, or fifty per cent a year, assuming that they were at birth of average length for their species and sex. This checks perfectly with the rate maintained by one of these four snakes for two weeks in July, following its first recapture. Five other juveniles, older than these, averaged 8.8 per cent increase per growing month. These figures for the sexually immature *Natrix sipedon* indicate an annual increase in length of about fifty per cent. In adult water snakes this rate is reduced to about a third, or even to much less.

SUMMARY

1. A simple and effective method of marking and numbering snakes has been described. This is useful where snakes are to be kept together in a laboratory or enclosure for observation or experiment, where they are to be released for studies of habits, or where for any purpose it is desirable to be able to identify individuals positively.

2. Seven species of snakes have been marked and released in the vicinity of the University of Michigan Biological Station in northern Michigan. The work was begun in 1929. To date, 811 field-collected specimens and several hundred young born in the laboratory have been released. The work has been largely centered on the garter snake *Thamnophis sirtalis* and the water snake *Natrix sipedon.*

3. " Returns " of those released in previous years have amounted to 6 and 8 per cent, respectively, in these two species.

4. Preliminary data from recaptured snakes indicate that wanderings may or may not be extensive and are not predictable.

5. Rate of growth computed from a small number of " returns " shows an increase of about 50 per cent a year in young of *Natrix sipedon,* and about 15 per cent in adults. For *Thamnophis sirtalis* these figures are approximately 30–40 per cent for young and 5 per cent for adults.

THE RATE OF PEAT GROWTH IN THE ERIE BASIN[1]

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The rate at which peat accumulates has been a matter of interest to geologists ever since the relation between peat deposits and coal beds has been appreciated. More recently the problem has assumed fresh importance because of the increasing use of peat microfossils as a key to post-Pleistocene climate.

In particular the relative percentages of different kinds of fossil pollen preserved in peat have been much studied in Europe. The purpose of such studies has been to interpret the changes in vegetation adjacent to the peat deposit during the course of its formation. Since most of the pollen preserved is brought in by the wind, the picture of changes appears to be somewhat generalized for the locality, and, therefore, it is often of value in interpreting climatic history. In a general way such evidence in Europe has supported the earlier findings of Blytt, Sernander and others regarding the shifts in moisture and temperature during postglacial times (Bülow, '29). In North America a number of pollen analyses have been made, some of which are not regarded by their authors as shedding light on climatic change. The senior writer, however, has now examined material from Pennsylvania, Ohio, Michigan, Indiana, Iowa and Arkansas. In every case he has obtained what seems like reasonable evidence of considerable climatic changes during postglacial times (Sears, '32). The most certain of these changes is a period of recent relatively dry climate followed by a gradual change to the somewhat more humid climate of the present.

In the case of deep columns of peat from Ohio, Michigan, Indiana and Iowa there appears to be good evidence of an earlier dry period separated from the one just described by a period of marked humidity. If these indications may be trusted the postglacial climate of North America has exhibited fluctuations similar to those of Europe. In Europe the postglacial climates have been accurately dated by de Geer's measurement of clay layers (Bülow, '29). Since this means of measurement has not been generally available in this country we have endeavored to find other means. Of these the most hopeful has seemed to be a determination of the mean rate of peat accumulation particularly in the Ohio-Michigan area with which we are most familiar. The following paper describes the results obtained in this connection.

Before proceeding with the paper acknowledgments should be made of

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[1] Contribution from the Botanical Laboratory, University of Oklahoma, No. 18.

the courtesy and cooperation received from the Department of Botany at the University of Michigan during the carrying on of the series of studies of which this is a part.

Previous Estimates

The available literature contains many suggestions as to the rate at which peat accumulates. These range from figures of 2 years per foot to 1650 years per foot, and are based upon diverse observations, calculations and conjectures. Some notion of these suggestions may be obtained from table I.

Table I. *Estimates of the time in years required to produce one foot of peat*

Years	Locality	Authority	Remarks
2	Ireland	Percy (Ashley, '07)	Doubtful
3.3-7.5	Hanover	Geikie ('03)	
4-5	Roman Roads	Percy (Ashley, '07)	
5	———	Ashley ('07)	Estimated maximum
5–10	———	Dana (Soper and Osbon, '22)	Estimated rate
6–8	Lake Constance	Geikie ('03)	
10	———	Ashley ('07), Moore ('22), Twenhofel ('26), White ('14)	Estimated average maximum
10	Warmburchen, Hanover	Haanel (Perkins, '27)	
10–13	Somme valley	Kolb (Geikie, '03)	
10–40	Europe	Koller (Ashley, '07)	
12	W. Rosshire	Geikie ('03)	
24–30	———	Twenhofel ('26)	Based on conditions at 20-25 feet
25–30	Danish Mosses	Geikie ('03)	
30–33	Swiss Jura	Lesquereux ('85)	
33–50	Switzerland	Haanel (Perkins, '27)	
75	———	Twenhofel ('26)	At 25 feet depth
100	———	Moore ('22)	Old compressed peat
100	Penna. ?	Lesquereux ('85)	
100	———	Twenhofel ('26)	Dense hard peat
100	———	White ('14)	N. temperate at 18 feet
*200	Ohio	Dachnowski ('12)	
200	Roman Causeway	Rennie (Ashley, '07)	
*300	Ohio-Michigan	Sears ('31)	Measured laminations
300–400	———	Lesquereux ('85)	"Immerged" peat
*555–1665	Great Lakes	Soper and Osbon ('22)	Calculated

In general it may be said that the most rapid estimates, even though coming from regions of maximum peat formation, are insufficiently supported. It is not safe to consider the time required for pits in peat beds to refill unless lateral slumping is absolutely prevented. Nor is it sufficient to note the depth of peat which now lies over roads or bridges whose approximate age is known. Roads and other structures frequently have sunk from sight in beds of peat.

The slowest estimates, those of Soper and Osbon ('22), are based upon calculations of postglacial time and apply to the Great Lakes region. Even if we had a general agreement as to the length of post-Wisconsin time, too little is known of the relative ages of deposits in the glaciated area to permit accurate calculations of this sort as yet. Moreover, there is good reason to believe that in the earlier, deeper phases of postglacial lakes the process of silting was much slower than the subsequent process of peat formation. In Mud Lake Ohio (Sears, '31) the silt and marl of 2 feet contain strata of fossil pollen which are equivalent to 10 feet of peat in the Bucyrus Bog.

It is, of course, generally recognized that climate within the peat-producing regions has a sensible effect on the rate of development. Eight feet of peat analyzed by Lane ('31) in Iowa probably is the equivalent of 17 in Indianapolis and 24 in Ohio as studied by the senior writer.

Disregarding the extremes, there is a tendency among the estimates to cluster about values of 100 to 500 years per foot for average well-consolidated peat. Lesquereux ('85), who was a careful observer, suggests rates of from 30 to 500 years per foot for peats of various regions. He further states that peat at the bottom of a deposit may be compressed to less than one eighth of its original volume. The estimate of Dachnowski ('12) of 200 years per foot has back of it an extensive knowledge of peat deposits in the central states.

Any attempt to solve this problem must recognize at the outset that it is very complex. Peat beds more than thirty feet in depth are common, but coal seams of greater thickness than six feet are not. Peat is a complex substance, biologically, physically and chemically. Any habitat in which it forms is subject to marked changes of a purely local character while the deposit is forming. Moreover, we are now certain that any peat beds of greater age than a thousand years have passed through periods of definitely different climates, with corresponding fluctuations in rate of accumulation. Until studies like the present are repeated elsewhere, this last factor has to be disregarded.

New Evidence

Knowing as we do that peat, lignite, and coal represent successive stages of change, marked by increasing compression over very long periods of time, it must be obvious that the so-called rate of peat accumulation cannot be a straight line function of uniform and constant slope. There is every warrant for the inference that is instead, a curve of exponential or logarithmic type. The problem then becomes, for practical purpose, a question of the rate of curvature. Is it rapid, or so slow that for long periods of time, such as 10,000 years, it may be dealt with practically as a straight line?

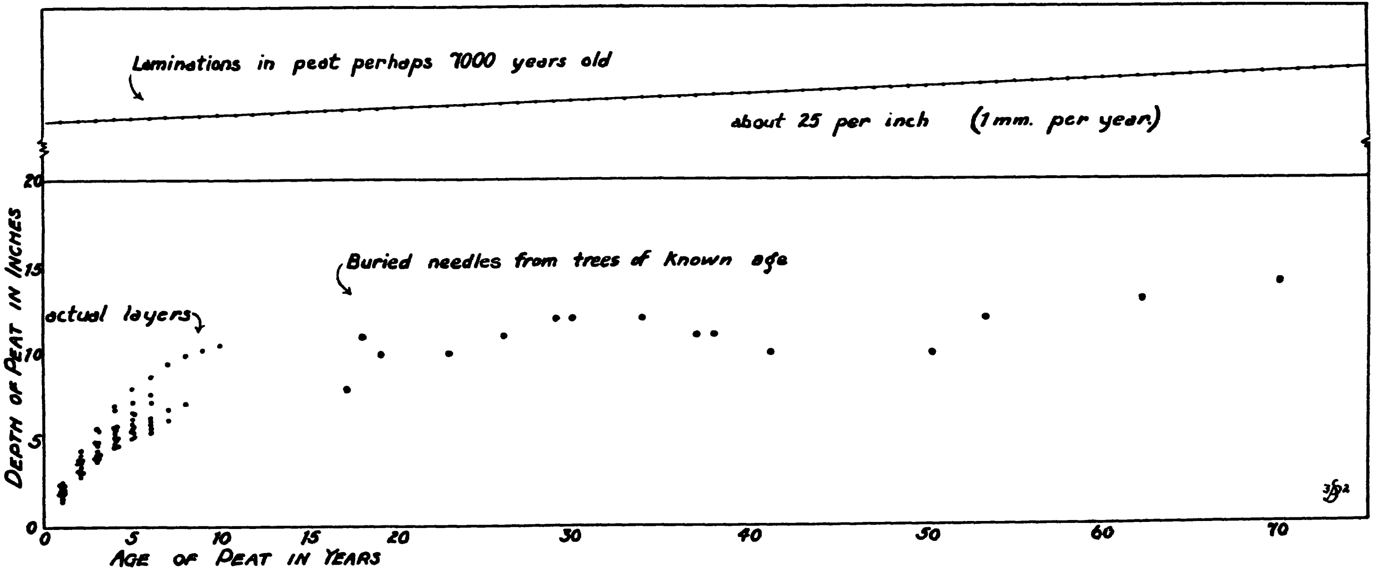

Fig. 1. Rate of increase in thickness of peat deposits with age. Data for first 10 years from measured layers; for 15 to 75 years from approximately dated conifer needles; for oldest peat from laminated material. Note especially rapid shrinkage during first 15 years, and similarity of slope in 15–75 year interval to that of 7,000 year old (early Atlantic or late Boreal) material.

The present paper presents data indicating that the latter is true, in general, for peat upwards of twenty five years old, in the Great Lakes area.

The first data obtained was from laminated brown peat 18–24 inches below the present surface of the Bucyrus Bog, in northern Ohio. This peat belongs to the oak-pine period (late Boreal or early Atlantic) correlative with a 24 foot depth near Wooster, Ohio, and a 17 foot depth at Indianapolis. It may reasonably be assigned an age of not less than 6000 to 8000 years. Its present shallow cover is due to extensive humification during the sub-boreal, and to fire and surface erosion.

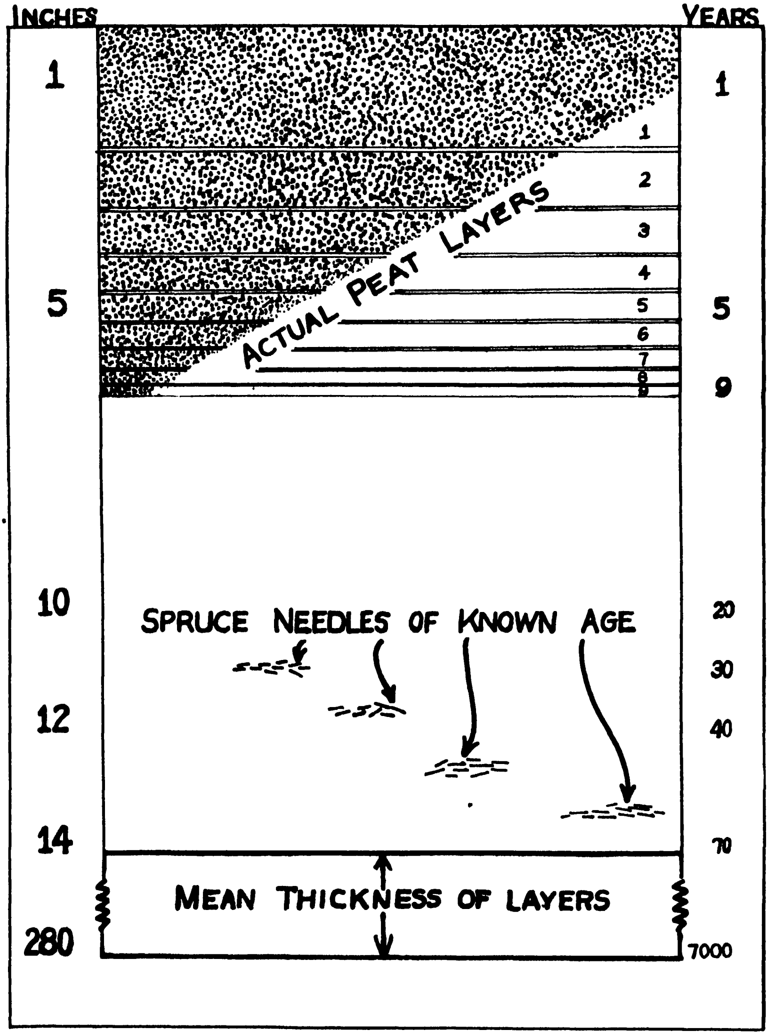

FIG. 2. Schematic section of upper part of bog showing actual rate of shrinkage of layers during first 9 years. Below, relative depths of conifer needles of different ages, also similar mean thickness of 70 and 7,000 year old annual layers.

The laminations of this peat were due to alternate layers of algal jelly and sedge leaves. In spite of considerable interweaving, there appeared on freezing, about 25 laminations to the inch (Sears, '32). Moreover, the mean distance between such layers of pollen as could be found in sections was about 1/25 inch. The inference was therefore drawn that these layers might be annual in character, and so represent a rate of about 300 years per foot of peat. (Cf. top of figure 1, bottom of figure 2.)

During the summer of 1931 the authors have studied the Mud Lake Bog north of Ann Arbor, Michigan.

Attempts to find definitely laminated peat were not successful. However, it was possible to separate the most recent layers for a distance of eight or ten inches down into the peat. These layers were measured with as much care as possible under field conditions and were found to decrease rapidly from a mean thickness of 2.1 inches to a mean thickness in the eighth to tenth layer of less than 1/4 of an inch. The data are listed in table II, and shown graphically in the accompanying charts, figures 1 and 2. It will be seen that this part of the curve is exponential in character.

TABLE II. *Distance in inches to base of successive peat layers, Mud Lake, Michigan*

	Layers									
Samples	1	2	3.	4	5	6	7	8	9	10
a	2.0	3.75	4.75	5.25	5.75					
b	1.5	2.75	3.75							
c	2.5	4.0	5.0	5.75	6.25					
d	2.5	4.5	5.75	6.75	7.25	7.75				
e	2.25	3.25	4.0	4.75	5.25	5.75	6.25			
f	2.0	3.25	4.25	5.125	5.875	6.375	6.875	7.125		
g	2.0	3.25	4.125	4.75	5.25	5.50				
h	1.875	3.125	4.125	4.875	5.625	6.125				
i	2.5	4.25	5.75	7.0	8.0	8.75	9.5	10.0	10.25	10.5
j	2.0	3.50	4.50	5.50	6.0					
k	2.25	3.75	5.0	5.875	6.625	7.125				
l	1.75	3.25	4.25	5.25	5.50	6.0				
m	2.25	4.0	5.0	5.875	6.625					

To secure data for greater depths isolated spruce and larch trees were selected in the bog. The age of each was then determined by means of an increment borer. Pits were sunk below each tree and a careful search made for needles as far down as they could be found. The results of these studies are listed in table III and shown graphically between the 15 and 75 year limits

TABLE III. *Depth of conifer needles deposited by trees of known age, Mud Lake, Michigan*

Age of trees in years	17	18	19	23	26	29	30	34	37	38	41	50	53	62	70
Depth of needles in inches	8	11	10	10	11	12	12	12	11	11	10	10	12	13	14

in figures 1 and 2. It will be noted that in contrast to the very rapid consolidation of the first eight or ten layers the subsequent change in the peat layers appears to be very slow. The approximate curve between 20 and 70 years differs very little from a straight line, having a pitch of approximately one inch in 20 years (fig. 1). If this be compared with the data obtained from laminated peat (top of fig. 1) believed to be between 6000 and 8000 years of age and at an equivalent depth of 24 feet, it will be seen that the change of slope is slight. The slope in the latter, it will be recalled, is one inch in 25 years.

It is, of course, possible to calculate a formula of exponential type whose curve will fit the data reasonably well. After considerable study, however, we have decided that the use of any formula at the present time would be premature. Any one familiar with curve fitting knows that numerous assumptions are involved. In the present case if a formula were assigned to the data it would carry implications regarding the slope of the peat accumulation curve back hundreds of thousands of years with increasing chances of error.

It seems best, under the circumstances, to satisfy ourselves with an empirical presentation of the data as obtained. Even with the most careful work, sources of error are numerous. The surface layers are not always easy to discriminate. Small wet-season fires may have altered the record. Shading by the spruces whose needles were used doubtless at times slows down the rate of peat growth below. Nor are the deepest traces of needles from a given tree always easy to locate.

CONCLUSIONS

Allowing for all of these difficulties, there appears to be a period of maximum compression during the first 15 to 20 years, and after that much slower compression. Comparing the measurements, such as they are, for the first 70 years with those from peat certainly between 6,000 and 8,000 years old, it does not appear far wrong to speak of a mean rate of peat accumulation of between 20 and 30 years to the inch for the past several thousand years, in the Great Lakes area. It is of interest to know that the application of this conventional rate to correlated deposits in Ohio has given a chronology for postglacial climates which is essentially that of the European periods of Blytt and Sernander as computed from clay varves by de Geer.

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ON THE ENUMERATION OF INSECT POPULATIONS BY THE METHOD OF NET COLLECTION

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The determination of insect population density in unit areas presents a vexatious problem to entomologists and ecologists. In the first place, the difficulties of collection of individuals on a unit area are manifold. Secondly, the problem of determining the trustworthiness of the data secured as a basis of generalization concerning areas of apparently similar character is a complex one. Of these two problems the latter will be of chief concern in the present discussion, especially since the importance of certain factors affecting the results appears not to have received the consideration from enumerators which scientific rigor would demand.

In any plan to secure a truly representative sample from a population of sedentary insects, considerations both of aggregation and distribution of the insects must be involved. At the symposium on statistical methods held during the 1924 meeting of the American Association of Economic Entomologists, several procedures of quantitative description were outlined. These apply quite well to relatively stationary forms. Very little has been offered, however, in the way of techniques suitable to the more active insects. Clearly, when some or all of the forms considered are freely moving, the added factor renders the solution of the problem much more troublesome.

Probably the most frequently used device for the collection of freely moving insects has been the insect net. This method has been severely criticized. Lockwood (1924) has written: " Attempts have been made to estimate the number of grasshoppers by collectors who used nets of the same size and made a certain number of sweeps in a given number of steps. . . . Sweepings made at different times of the day, under varying climatic conditions, in different crops, together with the varying speed of the operator, upset the uniformity of such reports." He considered the method " unscientific " and not to be relied upon in the collection of data. As an alternative he suggested a method which proved satisfactory for his immediate problem, but which is limited in its applicability to other insect forms. Many insects are considerably smaller and less conspicuous than grasshoppers, and the counting of these while freely moving would be difficult indeed. On the other hand forms which are readily detected in the open may completely evade notice while moving through heavy or even moderate stands of vegetation. It would be difficult indeed to estimate even a grasshopper population in a thick, mature stand of a crop such as alfalfa.

Attempts have been made to determine the population of a field by placing a chamber over a limited area and introducing some toxic agent to kill the insects present, the latter being recovered later and counted. The first objection to this method centers about the practical difficulty of placing the chamber over the vegetation without such disturbance of the insect population as would lead to the escape of many of the more active forms. Secondly, if fumigation is to be effective the chamber must fit the contours of the ground quite closely. A third objection arises from the difficulty of collecting all the insect forms from among the vegetation and debris of the substratum. Also, to render the conclusions drawn from such small areas applicable to field plots it is necessary to replicate the samples a large number of times. These area analyses are necessarily slow and frequently tedious procedures. To avoid discrepancies due to climatic and seasonal factors it is frequently necessary that the samples be taken simultaneously.

A review of the literature in the ecology of terrestrial insects reveals that despite its shortcomings the insect net is apparently still used very largely in the estimation of insect populations. Weese (1924), in discussing methodology, writes: " Throughout the period of study random samples were taken periodically. The unit sample from the herb and shrub strata was obtained by ten short sweeps through the vegetation with an insect net whose subcircular opening averaged 30 cms. in diameter." Blake (1926) used the same equipment and the same number of sweeps to estimate the population in the herb stratum. Carter (1927) in population studies of *Eutettix tenella* Baker, makes the following comment on collection technique: " Quantitative collections were made using one hundred sweeps of the net as a basis. This method is admittedly very inaccurate but so far is the best devised for an insect of this type." Smith (1928) and Shackleford (1929) both followed the lead of Weese. The number of sweeps in each case was increased to fifty. Each of these authors attempted to reduce the populations to a square meter basis by comparison with the results obtained by using a fumigation chamber. In the prairie environment a factor of unity and in the deciduous forest a factor of twelve was employed to convert the sweeping data to a square meter basis.

The desirability of accurate estimation of population density under *normal* conditions is just as great scientifically as under the economically stressful periods of pest outbreaks. Also the ecologist and field entomologist are keenly interested in the possibility of comparing safely the differences in population data secured under different conditions of time and space.

At times it seems desirable to examine rigorously our methods of securing data from which generalizations may subsequently be drawn. Grave doubts have existed in the mind of one of the authors for some time as to the adequacy of samples secured by sweeping, and the experimental work reported in this paper was the result of this distrust.

EXPERIMENTAL

In an endeavor to throw some light on the problem of the reliability of net collections, a study of sweeping yields was carried out under the supervision of one of us while at the Dominion Entomological Laboratory, Lethbridge, Alberta, Canada, during the summer of 1931. The area chosen was one on which alfalfa was growing, the selection being largely determined by the striking uniformity (*i.e.*, to the eye) exhibited as to thickness of stand, height and percentage of blossoms. The entire area of 2.25 acres bore a stand of approximately twenty-four inches in height and on the afternoon on which the collections were made was showing approximately forty per cent blossoms.

As a precautionary measure to maintain uniformity of conditions, a strip about ten feet wide around the outside of the plot was left undisturbed in making the collections. The sampling, carried out in units of twenty-five sweeps each, involved a total of one thousand sweeps of the net and covered the larger part of the area of the field. All the collecting was done by the senior author between the hours of 1:45 and 4:37 P.M. on August 12, 1931. A special effort was made to sweep at a constant rate, as well as to have the net travel a constant distance on each stroke and to a uniform depth into the herbage.

Five " American " nets with a subcircular diameter of fifteen inches were used for making the collections. Twenty-five sweeps were made with each net in turn, a sweep being taken with each alternate step. The nets were handed to an assistant who preserved them in the order in which they had been used. The material was then killed by placing the free end of each net in a large cyanide bottle. This was followed by the transference of the insects to numbered cans, the order of sweeping being thus maintained in the recording of the collections.

During the interval in which the material was in the cyanide bottles readings of temperature and relative humidity were taken. The former were determined by means of Tycos pocket case thermometers and the latter by a standard sling psychrometer.

To avoid sweeping the same area twice a route of sweeping as shown in figure 1 was followed. The lines of traverse in sweeping were sufficiently far apart (twelve feet) that there was no possibility of overlapping in the actual areas swept. An interval of approximately one hour intervened between sweepings at the points *a* and *b*. The time interval between sweeping at *b* and *c* was naturally somewhat shorter. However, the factor of disturbance by earlier nearby collecting was believed not to be serious in view of the distance apart of the lines of traverse.

When the collections were completed the cans were placed in cold storage until it was convenient to count and tabulate the material in each sample.

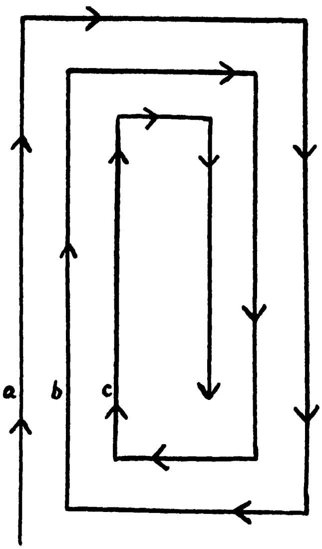

FIG. 1. The traverse lines along which the collections were made.

THE DATA

In table I a summary of the temperatures and relative humidities recorded is presented. It would seem that the variation in these physical conditions during the period of collection was not large enough to invalidate an assumption of reasonable homogeneity. There was a slight air movement during most of the afternoon, too slight to be called a breeze, and a few light clouds in the sky, but the day was primarily a " clear " one.

TABLE I. *Air conditions under which the collections were made*

Time	Temperature ° F.	Per cent relative humidity
1:45	78.0	32
2:10	77.5	35
2:35	79.5	34
3:00	80.0	29
3:25	78.0	36
3:50	79.0	31
4:10	80.5	29
4:37	80.0	29
Mean	79.06	31.9
Standard deviation	1.50	2.7
Coefficient of variation	1.89	8.6

An enumeration of the material secured is given by samples in table II. Certain of the more abundant insects are listed as species while in other cases

TABLE II. *A census of the collections by sample units of 25 sweeps each*

Insects captured	Sample number																																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	Total
Coleoptera—																																									
Sitona tibialis	1	3	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	0	1	1	0	2	0	7	0	0	0	1	24
Coccinellidae	2	1	0	0	0	0	0	0	0	2	1	1	1	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	1	0	0	1	0	0	5	1	1	21
Coleoptera misc.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	6
Diptera—																																									
Chloropisca glabra	4	17	1	0	0	0	1	0	3	4	0	4	3	0	0	4	0	4	0	1	0	1	2	5	5	3	1	0	0	2	4	1	2	0	1	2	2	0	1	2	80
Comptoprosopella vulgaris	1	2	1	0	0	1	0	0	0	0	0	0	1	1	0	0	2	1	0	0	0	2	1	2	4	3	0	0	0	1	1	2	1	0	1	0	1	0	1	0	30
Chironomidae	12	13	10	6	25	0	0	7	7	10	10	8	11	5	6	7	7	7	9	7	2	5	8	12	7	4	3	0	0	3	0	13	9	14	1	3	6	3	2	6	268
Dolichopodidae	6	3	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	2	3	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	22
Muscidae	10	8	6	4	5	5	0	3	6	2	10	9	7	3	5	13	13	10	10	9	23	18	19	28	14	3	11	9	13	22	4	0	7	15	11	10	5	13	11	9	383
Diptera misc.	0	0	1	0	2	1	1	4	0	0	0	1	0	1	0	0	4	8	3	1	2	0	2	0	2	1	3	2	4	6	0	2	3	0	4	1	0	3	7	4	73
Ephemerida—																																									
Ephemerida	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Hemiptera—																																									
Lygus elisus (adults)	12	13	10	7	7	14	13	7	15	15	9	3	11	9	8	7	5	6	8	9	7	8	8	10	9	8	4	3	2	6	12	10	9	4	14	16	4	6	8	8	342
Lygus elisus (nymphs)	7	5	9	5	3	0	14	6	7	5	28	1	3	0	0	1	1	5	1	1	1	5	2	0	1	0	3	1	0	3	0	0	0	1	0	0	0	2	0	1	122
Nabis ferus	0	3	4	3	1	4	3	0	4	3	3	3	2	2	1	0	2	4	1	11	6	2	4	7	3	4	3	1	4	8	6	5	5	6	6	1	4	3	2	4	138
Nysius ericae	1	0	0	3	0	0	1	2	0	0	2	0	0	2	1	0	2	3	1	2	0	0	2	2	0	0	2	1	0	1	0	0	0	2	2	0	0	0	0	0	32
Triphleps tristicolor	8	15	9	11	11	8	8	22	8	8	9	12	5	9	4	11	6	8	13	9	8	7	8	3	9	7	7	8	7	6	12	8	16	9	19	4	2	6	5	9	354
Hemiptera misc.	5	3	0	3	2	7	0	1	0	1	2	0	1	0	1	0	0	2	0	1	1	1	0	0	1	0	0	1	0	0	0	0	2	0	1	0	0	1	0	3	40
Heteroptera—																																									
Ceresa bubalis	0	1	0	0	0	0	1	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8
Cicadellidae	0	14	10	3	2	0	7	10	14	3	13	4	3	3	0	4	14	12	8	6	4	7	5	11	4	2	3	6	6	5	0	5	5	4	6	0	2	9	4	10	228
Hymenoptera—																																									
Apis mellifica	3	4	3	3	4	10	6	14	9	4	8	6	4	7	6	5	10	3	13	9	11	13	14	6	9	12	9	11	13	7	7	1	7	7	7	3	2	8	11	15	302
Chalcididae	4	1	0	4	3	2	5	0	7	8	11	8	4	2	4	7	3	2	2	0	1	0	0	4	0	4	0	2	2	0	0	0	0	0	0	0	0	0	2	0	92
Other parasitic hymenoptera	0	8	3	0	5	6	5	10	6	5	5	4	1	1	0	2	1	2	1	3	4	5	0	3	0	0	1	0	0	1	4	4	0	3	2	0	2	0	0	2	99
Hymenoptera misc.	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	4	2	1	1	0	1	0	3	0	0	0	2	1	0	0	0	0	20
Lepidoptera—																																									
Lepidopterous adults	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	2	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	7
Lepidopterous larvae	1	4	2	3	0	4	2	1	0	1	1	1	3	0	2	2	4	2	1	3	4	0	2	1	5	1	0	4	1	0	3	0	3	1	1	4	0	1	0	3	71
Neuroptera—																																									
Neuroptera	0	2	1	0	1	0	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	11
Orthoptera—																																									
Conocephalus fasciatus	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	1	8
Melanoplus sp.	3	2	2	1	1	0	1	1	0	1	1	1	2	2	0	0	0	0	1	1	2	0	0	1	2	1	0	0	0	0	0	0	1	0	0	2	0	0	0	0	29
Thysanoptera—																																									
Anaphothrips striatus	10	7	11	12	20	0	0	60	25	6	16	29	4	9	8	23	27	33	24	22	1	18	24	14	13	17	12	14	9	17	7	8	11	9	18	4	5	6	18	9	580
TOTALS	92	130	83	72	92	63	71	152	113	78	130	100	67	57	46	88	102	114	97	97	79	93	107	115	98	71	64	64	64	88	66	62	81	77	97	61	36	65	74	88	3394

where the frequency of occurrence of species is very small the material has been classified according to order or family only.

A selection involving ten of the more abundant species and other taxonomic groups has been made. For these as well as for the total number of insects in each collection the mean, standard deviation, and the coefficient of variation of the 40 samples have been calculated. These statistics are presented in table III.

TABLE III. *Statistics of population density for 40 collections each for ten insect groups and the total number of all insects*

Insect groups	Mean number captured[1]	Standard deviation[1]	Coefficient of variation
Anaphothrips striatus	14.50 ± 1.16	10.858 ± 0.819	74.9%
Apis mellifica	7.55 ± 0.40	3.715 ± 0.280	49.2
Chironomidae	6.70 ± 0.52	4.900 ± 0.370	73.1
Cicadellidae	5.70 ± 0.43	4.069 ± 0.307	71.4
Lepidoptera (larvae)	1.78 ± 0.16	1.458 ± 0.110	82.1
Lygus elisus (adults)	8.55 ± 0.37	3.514 ± 0.265	41.1
" " (all)	11.60 ± 0.71	6.633 ± 0.500	57.2
Muscidae	9.58 ± 0.65	6.115 ± 0.461	63.9
Nabis ferus	3.45 ± 0.24	2.247 ± 0.169	65.1
Triphleps tristicolor	8.85 ± 0.42	3.934 ± 0.297	44.5
Total group	84.85 ± 2.52	23.667 ± 1.785	27.9

[1] ± probable errors.

THE STATISTICAL PROBLEM

a. Heterogeneity of Population Density

The evaluation of the reliability of any particular statistic (such as population density) in relation to the number of individuals on which it is based does not present any difficulty provided that conventional assumptions attending the calculation of standard errors (or probable errors) may validly be made. Thus the standard error measures the trustworthiness of a statistic as a basis of generalization, so far as *random* errors of sampling are concerned. In the present problem the variation in the mean number of insects from a given number of samples would be given by the standard error of that mean, provided that the samples differed solely by errors of random sampling from a homogeneous population. The wary entomologist will at once raise the question as to whether such an assumption can be made even in a uniform sampling procedure from an apparently homogeneous field. Remembering that apparent homogeneity of stand of the alfalfa does not necessarily imply homogeneity in the density of the insect populations inhabiting the area, it is clear that an independent test of the latter must first be made.

In a field of uniform population density of any insect, sweeps of the collecting net should provide at all points estimates of that population density that differ solely by errors of random sampling. Under such conditions there would not be any real correlation between the yields of successive sweeps.

On the other hand, if the population density of the insect be greater in certain areas than in others, then the net collections should show a tendency to be correlated with the space factor. In other words, successive sweeps on any given traverse should show a correlation between their yields of the insect in question should its distribution be heterogeneous.

In the experiment detailed herein the individual sweep of the net did not provide the unit of enumeration of population, 25 successive sweeps being combined to form each unit. Clearly the effect of such combination must be to reduce the correlation between successive units, for each unit may embrace areas of both high and low population density. Therefore the correlation between successive sweeps must logically be assumed to be greater (*i.e.*, more positive) than that between successive units of 25 sweeps each. Thus a correlational measure of heterogeneity based on the units of enumeration employed herein must underestimate the true heterogeneity of distribution of the insect groups considered.

The method employed here in securing the correlation between the insect group totals in successive units is that of considering all possible pairs of contiguous collections. Thus the first and second units provide the first pair, the second and third the second pair, the third and fourth the third pair, and so on. For 40 such successive units, there will obviously be 39 pairs to the correlation surface, all but the first and last collections in the entire traverse being considered both as a first and as a second member of a pair. This correlation surface may be rendered symmetrical by reversing the order of all combinations and the significance of the observed coefficients tested for accordingly. The correlation coefficients, with their corresponding probabilities as random deviations from zero, are given in table IV.

TABLE IV. *Correlation coefficients between successive collection units, measuring heterogeneity of insect population density*

Insect group	r	$p_{r=0}$
Anaphothrips striatus	+ .086	.55
Apis mellifica	+ .334	.02
Chironomidae	+ .118	.41
Cicadellidae	+ .125	.38
Lepidoptera (larvae)	— .335	.02
Lygus elisus (adults)	+ .299	.03
" " (all)	+ .291	.04
Muscidae	+ .469	.00
Nabis ferus	+ .188	.18
Triphleps tristicolor	— .173	.22
Total group	+ .365	.01

There can be little doubt of the existence of heterogeneity of distribution of the insect population in the apparently uniform alfalfa field considered in this study. This is true of all insects taken together, and of the Muscidae, Lepidoptera (larvae), *Apis mellifica* and *Lygus elisus*. The correlation for the lepidopterous larvae is of interest particularly because of its negative character, indicating a periodicity in heterogeneity tending to correspond to the distance of the unit collections of 25 sweeps. Such must be a chance phenomenon.

Although the correlations deviate from zero greatly enough to be significant in but 6 out of the 11 groups studied, it must be remembered that the large number of sweeps per collection has rendered the correlations less sensitive as a measure of heterogeneity than smaller collection units would be. Of the 5 " insignificant " coefficients, 4 are positive, which is indicative again of heterogeneity. In all, the evidence points to the same lack of homogeneity as has long been familiar to agronomists as a character of crop yields on apparently uniform fields. The statistical aspects of the latter problem have been thoroughly considered by Harris (1915, *et seq.*), to whose papers the interested reader is referred. It is of considerable interest to note the extension of this concept to entomological problems.

b. The Variation in Sweep Yields

A very pertinent question asked by many a practical worker is: How large a sample must I use? In the present investigation the question might take the form to the entomological field man: If a sweeping method must be employed to estimate insect populations, how many sweeps will be necessary to afford a reliable index of the population density, both as to the number of species present and their relative abundance? The statistician's answer to this question must depend upon a knowledge of two factors: (*a*) the extent and form of variation in the yields of individual sweeps or composite units, and (*b*) the tolerance of error or degree of accuracy desired in the statistics to be calculated.

In the problem under consideration the numbers of individuals in various insect groups are available for each of 40 units of collection. The magnitude of variation may be calculated readily by means of the standard deviation,

$$\sigma_x = \sqrt{\frac{\sum (x-\bar{x})^2}{N}} = \sqrt{\frac{\sum (x^2)}{N} - (\bar{x})^2},$$

while the form may be judged approximately by preparing histograms for each insect group. The statistic to be considered here is the mean number of insects per unit of collection (25 sweeps), and since the form of distribution of means is approximately " normal " for even quite skew distributions of individuals, the histograms referred to above need not be prepared in arriving at a first approximation to the desired result. The range of variation of means may be taken roughly as 4 times the standard error to cover the central 95 per cent of the distribution. Therefore, with the mean of all 40 collections for each insect group and the standard deviations given in table III, it becomes a simple matter to find the number of units per combination to hold the variation of means of those combinations within a given range, *provided it may be assumed that random errors only differentiate the members of a combination.*

Let $\bar{x}_{40}$ be the mean of all collections, $\bar{x}_n$ be the mean of n samples from the 40, σ the standard deviation of the 40 yields. Then if the range of variation (as above) in $\bar{x}_n$ should not exceed y per cent of $\bar{x}_{40}$, we have

$$\frac{\sigma}{\sqrt{n}} = \frac{y(\bar{x}_{40})}{4 \times 100} \,.$$

Or again, if V be the coefficient of variation of the 40 yields for each insect group,

$$V = \frac{y\sqrt{n}}{4}$$

and

$$n = \frac{16\,V^2}{y^2} \,.$$

Substituting the statistics given in table III for the ten selected groups and the total, the desired values of n to the nearest whole number for ranges of both 10 per cent and 50 per cent error are as given in table V.

TABLE V. *Number of collections of 25 sweeps each necessary for the restriction of error ranges to 50 per cent and 10 per cent of the grand means*

Insect group	$n_{50\%}$	$n_{10\%}$
Anaphpthrips striatus	36	897
Apis mellifica	15	387
Chironomidae	34	856
Cicadellidae	33	816
Lepidoptera (larvae)	43	1079
Lygus elisus (adults)	11	270
" " (all)	21	523
Muscidae	26	653
Nabis ferus	27	679
Triphleps tristicolor	13	316
Total	5	124

These results may well be astonishing to entomologists. In no case can accuracy to within 10 per cent of the true value be secured from less than 120 collections of 25 sweeps each. If so low a degree of accuracy as that within 50 per cent of the true value (assuming x_{40} to be that value) be striven for, as many as 43 collections of 25 sweeps of the net each would be necessary for the lepidopterous larvae, while for the ten sub-groups considered the average number of collections would have to be 26. This corresponds to 650 sweeps of the net!

Despite the rather insidious danger of spurious interpretation attaching to the coefficient of variation, this statistic is still considerably used by biologists as a relative measure of dispersal. For those who approve its use it may be indicated that, in the present connection, it loses its objectionable features since the variable is itself a pure number whose range logically commences at zero in all cases.

The coefficient of variation between unit yields may be expected to decrease as the number of sweeps per collection unit is increased, in proportion to the square root of the factor of increase (provided complete randomization of sweeps is attained). Thus if increase in number of sweeps per collection unit is made by assembling contiguous units of smaller numbers of sweeps, and the fall of the coefficient of variation does not accord with the above rule, then evidence is given of heterogeneity of population density. This is illustrated in table VI where the actual change in V is given in arabic numerals and the expected change (assuming homogeneity of population density) is given in italics.

The consistency of the nature (sign and magnitude) of the discrepancies between actual and expected values in table VI with the coefficients of correlation in table IV will be noted immediately. Also the large actual variation between yields of 200 sweeps each will impress the observer with the fallacy of attempting the enumeration of insect populations in such a habitat as an apparently uniform field of alfalfa by making anything less than a very large number of sweeps throughout the entire area.

TABLE VI. *Comparison of the coefficients of variation for several sizes of collection units*

Insect group	Number of contiguous sweeps per collection unit			
	25	50	100	200
Anaphothrips striatus	74.9	47.8 (*53.0*)	36.9 (*37.4*)	24.1 (*26.5*)
Apis mellifica	49.2	39.1 (*34.8*)	29.2 (*24.6*)	20.1 (*17.4*)
Chironomidae	73.1	50.1 (*51.7*)	30.1 (*36.6*)	28.2 (*25.8*)
Cicadellidae	71.4	49.4 (*50.5*)	39.4 (*35.7*)	26.0 (*25.3*)
Lepidoptera (larvae)	82.1	41.3 (*58.1*)	35.9 (*41.1*)	18.6 (*29.1*)
Lygus elisus (adults)	41.1	36.6 (*29.1*)	21.1 (*20.6*)	16.2 (*14.6*)
" " (all)	57.2	42.8 (*40.4*)	38.4 (*28.6*)	30.9 (*20.2*)
Muscidae	63.9	57.3 (*45.2*)	43.6 (*32.0*)	39.6 (*22.6*)
Nabis ferus	65.1	44.9 (*46.0*)	38.5 (*32.6*)	29.2 (*23.0*)
Triphleps tristicolor	44.5	29.1 (*31.5*)	24.3 (*22.2*)	15.4 (*15.8*)
Total group	27.9	22.0 (*19.7*)	17.6 (*14.0*)	13.5 (*9.9*)

DISCUSSION

There are many respects in which the habitat chosen for this study of the efficacy of net collection as a basis of the estimation of insect populations in herbage approached perfection. The very low variation in the edaphic factors of light, temperature, humidity and air movement, plus a constancy in sweeping technique striven for by the collector, must have considerably reduced the shortcomings normally pertaining to the method of collection. Such variation as is revealed by the results must surely be lower than might more generally be expected.

The authors are fully aware of the many factors only partially controlled in the present investigation which would considerably augment variation in the yields. These factors have been suitably considered by de Long (1932) and need not be repeated here. Indeed, it is beside the point to do so, since the present study aims to set forth measures of variation (which would appear to approach a minimum for general field work) and discuss their practical significance rather than the causes of variation.

The data presented herein show clearly, at least for several of the insect groups considered, that their populations in alfalfa fields are by no means uniformly distributed even under apparently uniform conditions. This concept of heterogeneous population density is by no means novel. A consideration of the oviposition habits of many insect forms would lead *a priori* to the expectation of lack of homogeneity of distribution of the immature stages. When they later transform to adult stages their spread may be slow in many, if not most, cases. Beyond this, however, there are many factors no doubt, as yet unmeasured, which are conducive to the heterogeneity which has been statistically measured in the foregoing section. The importance of the accurate demonstration of heterogeneity in insect population density lies in the warning it gives that field collections must be representative of all sub-areas and uncorrelated with space factors.

The comparative enormity of variation between yields of collection units of 25 sweeps each in this study indicates that net collections must be very large in number of sweeps before any trustworthy enumeration of the insect fauna of such habitats can be formed. Indeed the number of sweeps required for even a 50 per cent error range (as of the true mean) is so large as to preclude the usefulness of the technique for census purposes under most practical conditions.

It would seem highly probable that areas of mixed vegetation would show greater variation than that encountered in a pure stand of a host plant of uniform development.

SUMMARY

Sweeping with an insect net was employed in an alfalfa plot with a view to determining the accuracy of this technique for purposes of enumerating insect populations. The work was carried on in such a manner as to insure that the principal variable was the distribution of the insects in the area. Forty units of twenty-five sweeps each, taken progressively along a line of traverse covering almost the entire field of 2.25 acres, provided the basic data. The insects in each collection were segregated into 28 taxonomic groups, 3394 insects being counted in all. A statistical analysis of the data for the total number of insects in the 40 collection units and also in the ten most abundant taxonomic groups is reported.

Heterogeneity of population density over the entire field is proven for 6 of the 11 classifications by significant coefficients of correlation, reaching + .47 for the Muscidae, and must be anticipated as being higher if enumeration by single sweeps could be considered.

Variation between the yields of successive collection units ranges from a coefficient of variation of 28 per cent for the total group to 82 per cent for lepidopterous larvae, and averages 62 per cent for the ten more abundant taxonomic classifications. The number of collections of 25 sweeps each necessary to secure a reduction of error range of the mean to 50 per cent of the "true" value, ranges for the groups as above from 5 to 43 with an average of 26. For a reduction of the error range to 10 per cent the number of collections must vary from approximately 124 to 1079, involving from 3,100 to 26,975 sweeps of the net! Therefore the use of the sweeping method for purposes of comparing different types of environment under the same conditions, or the same type of habitat under different conditions, would appear to have little quantitative value unless based upon extensive collections.

The calculation of the number of collections necessary to confine errors within certain ranges involves the assumption of lack of correlation between the yields of the collections averaged. Considerable evidence being given that this assumption is hazardous, contiguous collections should therefore not be used. It is a matter of considerable importance, then, that the principle of randomization of collection be observed where dependence in census work must necessarily be placed on the method of collection by sweeping with insect nets.

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EFFECT OF FREQUENT CLIPPING ON THE DEVELOPMENT OF ROOTS AND TOPS OF GRASSES IN PRAIRIE SOD[1]

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A study has been made of the regeneration of bluestem grasses in exclosures in continuously grazed native pastures. The persistence of remnants of the bunches or mats of sod in old pastures for a long period of years is of interest, as is also their gradual but slow rate of recovery under protection when they are greatly weakened. Even in low, fertile, well watered soil, a period of three or four years must elapse before such species as *Andropogon furcatus* and *Sorghastrum nutans* produce the usual abundance of flower stalks and large quantities of viable seed. The first summer only a poor growth of scattered foliage outlines in a fragmentary manner the location of the underground parts that have been thoroughly weakened by continuous depletion of their food supplies. A second growing season shows a marked filling in of the sodded areas or clumps and about half the normal production of foliage. During the third summer the area is further extended and at least a few flower stalks and some seed are usually produced.

During this process of recovery it was repeatedly noticed that these grasses were much more subject to wilting than were similar species in adjacent areas that had not been grazed. The leaves would roll or fold and many of the lower ones dry and lose their green color. The evidence pointed clearly to a meager or inefficient root system.

The quantitative development of roots or their degree of deterioration is difficult to study under field conditions because of the labor involved in separating the living rhizomes and fibrous roots from those that are dead and from partially decomposed fragments of leaves, etc., intermixed with them. Earlier experiments where blocks of sod were transplanted showed that new roots were rapidly developed (Clements and Weaver, '24). Hence it was decided to select representative samples of the several most important native grasses, cut out blocks of soil containing them, and transplant these into large containers filled with soil free from roots and debris. One lot of each was to be clipped at 14-day intervals and the duplicates were to be grown as controls.

Grazing is a more or less destructive process since it periodically removes much of the photosynthetic area of the plants and an abrupt decrease in the photosynthetic activity causes a corresponding decrease in the growth of the

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roots. Continued defoliation will cause destruction of the root system and result in death. Hence, unless reasonable precautions are taken, the effects of grazing are likely to become cumulative and cause serious deterioration of the range.

The effect of the removal of the photosynthetic area upon the growth of the tops has received considerable study. Many data have been obtained from clipping vegetation in the western two-thirds of the United States. They show that the yield and vigor of the vegetation varies inversely with the frequency of clipping.

Crozier ('97) in Michigan, found that frequent mowing of various cultivated grasses reduced the yield to one-fourth normal and that the yields were highest on the plots clipped least frequently.

Sampson ('14), working in the Wallowa National Forest in Oregon, found that when *Festuca viridula,* one of the chief forage species, was clipped three times each season during a period of three consecutive years, the vegetative growth decreased in abundance each successive season.

Sarvis ('23), working in the mixed prairie of North Dakota, found that *Stipa comata* disappeared entirely under frequent harvesting and that various other grasses showed lowered vitality. The highest yields were obtained from plots clipped at 40-day intervals and the lowest from those clipped every 10 days.

Sampson and Malmsten ('26), in a study of forage species in Utah, found that the removal of the herbage four or more times in a season resulted in a sharp decline in yield and in a marked shortage of the life of the vegetation. *Stipa lettermani* and *Agropyron violaceum,* clipped five times annually for three successive years, yielded in the third year only 12 and 9 per cent respectively, of the amount of herbage that was produced during the first year of clipping. A short-lived perennial, *Bromus polyanthus,* died under similar treatment.

McCarty ('27), working in Colorado, judged yields on a basis of their calculated values for the second year of treatment, thus attempting to eliminate seasonal variation from year to year. " Quadrats of *Agropyron smithii,* harvested four times during one year, yielded 84 per cent of their calculated value during the second year of treatment. Quadrats harvested seven and eight times in one year yielded, respectively, 50 per cent and 40 per cent of their estimated values during the succeeding year."

Graber *et al.* ('27), in Wisconsin, showed that the productivity of well established bluegrass sod, following two years of frequent cuttings, was reduced to less than one-fourth that of adjacent bluegrass, *Poa pratensis,* cut but once annually at maturity. Similar results were obtained with red top, *Agrostis alba.*

Aldous ('30) applying clipping treatments at two-week intervals in Kansas, found that the density of the vegetation decreased about 60 per cent in three seasons. Clipping at three-week intervals resulted in only a 13 per cent reduction.

Numerous other researches bear out the conclusions of these investigators. Ellett and Carrier ('15), Stapledon ('24), Stapledon and Beddows ('26), Sturkie ('30), and Hanson *et al.* ('31) are all in agreement that the total yield of forage is reduced by frequent removal of tops.

Much less work has been done to show the deleterious effects of clipping on root development. This has probably been due to the difficulty of observing closely the parts below ground.

Fitts ('25), working with fine turf grasses, found that the length of the roots increased in relative proportion to the height to which the tops had grown.

Stapledon and Beddows ('26) showed that the repeated cutting of orchard grass, *Dactylis glomerata,* during the growing season not only decreased the amount of hay and aftermath crop but it also reduced the root systems of the plants and retarded their growth early the following spring.

Sampson and Malmsten ('26) state that any cropping which results in the reduction of the aerial growth of grasses is reflected in the root development and in the quantity of food stored in the underground parts.

Graber *et al.* ('27) found that frequent and immature cutting of bluegrass reduced the amount of rhizome and root growth and increased the prevalence of weeds when compared with similar bluegrass cut at maturity.

Pierre and Bertram ('29) studied the storage of organic foods as they affect the tops and roots of kudzu, a leguminous vine. They found that the roots of plants cut six times per season decreased in weight during a period of two years, while those from plants receiving four cuttings increased about 150 per cent. The reserves of starch and nitrogen were less than one-half as great in the roots of plants receiving six cuttings as in those receiving four. Similar studies on organic food reserves have been made by Graber *et al.* on alfalfa ('27).

It has been shown by Parker and Sampson ('31) that a single harvesting of the tops of *Stipa pulchra* and *Bromus hordeaceous* resulted temporarily in the cessation of root growth. Robertson ('32) found that the rate of growth of the roots of *Bromus inermis* diminished gradually as a result of clipping. Growth then ceased for 12 days before the roots started to die back from the tips.

Harrison ('31) clipped grasses at different heights and concluded that the amount of roots increased with the height to which the grasses were clipped.

Robertson ('32) observed that in general root penetration of seedling grasses was retarded from 35 to 62 per cent as a result of frequent clipping, and that the dry weight of the roots was reduced from 66 to 98 per cent.

Investigators are in agreement that the more frequent and drastic the cutting treatment the less is the yield of tops, rhizomes, and roots (*cf.*, Nelson, '25; Albert, '27; and others). An exceptional finding is that of Laird ('30) who worked in the sandy soils of Florida. He states that "the largest and deepest root system of sod-forming grasses is not necessarily associated with the best and most vigorous top growth. . . . mowing of centipede and Bermuda grasses increased the root growth. . . ."

METHODS

Representative bunches or clumps of several species of native grasses were selected in duplicate and removed from the unbroken prairie sod. This was done between June 28 and July 24. The species included were big bluestem, *Andropogon furcatus,* tall panic grass, *Panicum virgatum,* little bluestem, *A. scoparius,* slender grama, *Bouteloua curtipendula,* and a prairie drop-seed, *Sporobolus heterolepis.* The first two were taken in duplicate sets and will be designated as series 1 and 2. The prairie from which the preceding dominant grasses were taken has never been disturbed except by mowing. In addition, Kentucky bluegrass, *Poa pratensis,* blue grama grass, *Bouteloua gracilis,* buffalo grass, *Bulbilis dactyloides,* and western wheat grass, *Agropyron smithii,* were secured from a native pasture. Here the usual tall-grass prairie species had practically disappeared before these invaders. The pasture had not been grazed, however, since the previous summer and the grasses were all in excellent condition.

The sods of *Andropogon furcatus* were cut so that they each had a surface area of 25 square inches and a depth of 4 inches. Those of the other species had a similar surface area but a depth of 5 inches. Since all of these species renew activity about April 15, except *Poa pratensis* and *Agropyron smithii* which break their winter dormancy nearly a month earlier, they had already made a good growth. The height of the foliage at the time each species was transplanted and the height to which it was clipped are shown in table I.

TABLE I. *Condition of the grasses at the time of transplanting. The figure in parentheses indicates the series.*

Species	Date of transplanting	Height tops, in.	Height clipped, in.
Andropogon furcatus (1)	June 28	14	1.5
Andropogon furcatus (2)	June 28	20	1.5
Bulbilis dactyloides	June 28	6	0.5
Panicum virgatum (1)	June 28	15	1.5
Poa pratensis	July 10	4	0.5
Sporobolus heterolepis	July 10	14	1.0
Agropyron smithii	July 10	16	1.0
Bouteloua gracilis	July 11	8	0.5
Andropogon scoparius	July 11	10	1.0
Panicum virgatum (2)	July 24	34	1.5
Bouteloua curtipendula	July 24	14	1.0

The sods were transplanted into galvanized iron containers which were filled with a rich loam soil mixed with one-fifth of its volume of sand. The containers had a cross-sectional area of one square foot and varied from 2 to 2.5 feet in depth. Each sod was placed with its surface 0.5 inch below the top of the container, thus permitting watering without run-off, and the soil was firmly compacted about it. An opening made in the side near the bottom of each container insured proper drainage and aeration. The containers were placed in a trench 14 inches wide which was excavated in a bluegrass lawn and soil was packed around them. The trench was just deep enough so that the level of the tops of the containers was 2 inches above the general soil surface. Thus, surface water following heavy showers was prevented from running into them and a drain made in the trench prevented any accumulation of water. Thus the grasses were grown with the same variations in sunshine and temperature that they would have had in the prairie.

The soil was kept at an approximate optimum water-content for growth by frequent watering, the sods that were producing an abundance of foliage requiring water in larger amounts than the clipped ones, as was shown by soil sampling.

After the plants had become well established, one lot of each species was clipped every 14 days. The foliage produced at each clipping was placed in a drying oven at a temperature of 85° C. for 48 hours and the dry weight determined.

The grasses were permitted to grow until October 5 to 10, when the containers were removed from the trench and placed in a large trough. They were cut open on one side and a gentle stream of water was used to wash away the soil. Such care was taken that the roots were secured almost if not quite in their entirety. The muddy water drained through a screen of fine mesh which was used to catch any broken fragments, but in any case there were but very few small pieces found. The process of washing away the soil required much care, and a whole day to lay bare the root system of a single species.

The tops were removed and their dry weight determined. The flower stalks and foliage of the unclipped grasses were, with a single exception, obtained separately. The roots were also cut away from the base of the original block of soil. The volume of the roots was obtained after all surface water had been removed by pressing the roots repeatedly for a few minutes between blotting papers.

A simple but accurate apparatus was devised for determining the volume. A glass jar 10 inches high and 3 inches in diameter had attached to it a small glass U-tube which served as a siphon. The jar was filled with water which was then allowed to run out to the level of the short end of the tube outside the jar. When the roots were then submerged the overflow water was caught directly in a small graduate. In measuring the volume of small root masses, the roots were placed in a 25-cc. graduate and water was allowed to drop slowly from a burette until it reached a certain mark above the level of the roots. Care was taken to exclude bubbles of air. The volume of roots was the difference between the number of cubic centimeters of water added and the total volume of water plus the submerged roots in the graduate.

Parts of typical roots of both the clipped and unclipped *Panicum virgatum* and *Poa pratensis* were selected for study. They were the portions of the roots between the fifth and tenth centimeters from the tip. These were killed in formalin-acetic-alcohol and embedded in paraffin. Slides were prepared from this material.

RELATIVE DEVELOPMENT OF TOPS AND ROOTS

Growth of tops began almost immediately after the sods were transplanted, except in *Agropyron smithii* which was more mature. Here there was a delay of two weeks. Measurements made on alternate days (June 30–July 16) showed that the rate of growth, while varying considerably for the different species, was remarkably uniform within the species. The average daily rate of elongation during the first 16 days, for example, varied from 1.7 cm. for *Panicum virgatum* to 2.3 cm. for *Andropogon furcatus.*

Big Bluestem. The unclipped *Andropogon furcatus* made a luxuriant growth throughout the period of the experiment. Flower stalks began to appear on August 19 and when the grass was harvested on October 5, 45 had developed. They had an average height of 69 inches. Large, well developed fruits were produced in abundance. At this time the grass was taking on the reddish autumnal color similar to that in the prairie. The dry matter produced weighed 216.34 grams.

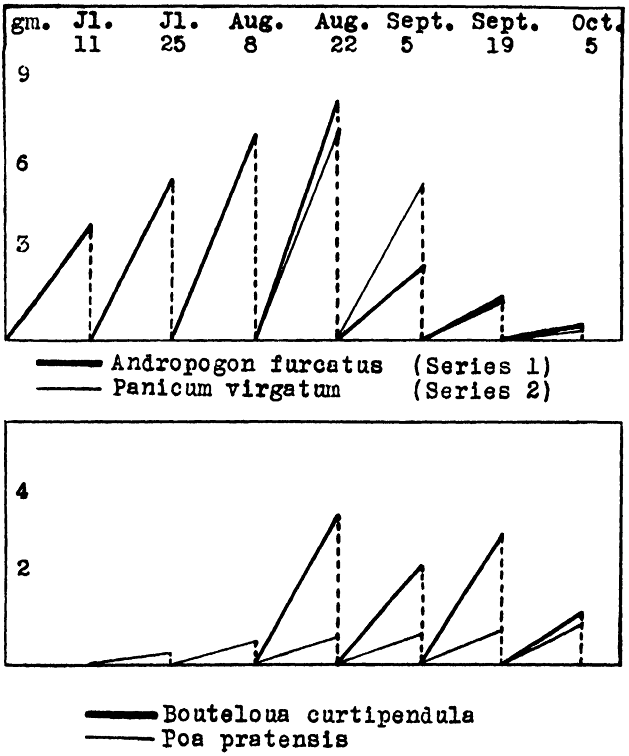

FIG. 1. Amount of dry matter produced by the several grasses at each clipping.

The amount of growth of the clipped grass increased gradually for the first four clippings. After the fourth clipping, however, both rate of growth and amount of dry matter decreased considerably (fig. 1). The stand of grass was thinner after the fourth clipping since some stems did not recover and others made a growth of only 1 to 3 inches. Other stems grew well even after the fifth and sixth clippings, but the growth was not as great as that following the earlier ones. The total amount of dry matter produced by the clipped sod was 31.32 grams, which was only 14.5 per cent as much as that of the control.

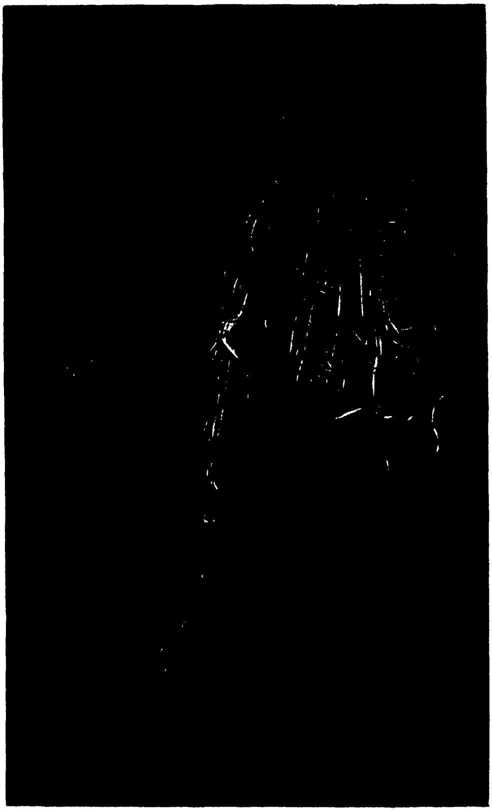

FIG. 2. *Andropogon furcatus* about 3 months after transplanting. Plants on the left have been repeatedly clipped.

The roots of the control formed a dense mat throughout the whole volume of soil. Those of the clipped sod were not nearly so abundant (fig. 2). Practically all of those of the control and about 30 per cent of the others extended to the bottom of the container, which was 2 feet deep. While the photograph shows the length and width of the mass of roots, it does not show the thickness of the mat, which was more than an inch when the roots were

TABLE II. *Amount of dry matter in grams produced at each clipping; also total amount for clipped and control plants, and percentage of dry weight of clipped compared to unclipped plants.*

Date of clipping	July 11	July 25	Aug. 8	Aug. 22	Sept. 5	Sept. 19	Oct. 5–10	Total dry weight of tops			Per cent
								Clipped	Control		
Andropogon furcatus (1).......	4.12	5.91	7.41	8.52	2.88	1.86	.62	31.32	Lvs. 53.54 Stems 162.80	216.34	14.5
Andropogon furcatus (2).......	4.14	5.83	7.33	6.26	2.92	1.39	.28	28.15	Lvs. 41.83 Stems 111.26	153.09	18.4
Bulbilis dactyloides............	1.12	3.52	4.51	3.91	3.44	3.22	.45	20.17	Lvs. 31.95 Stems .00	31.95	63.1
Panicum virgatum (1).........	.57	1.75	2.73	4.12	2.37	.38	.08	12.00	Lvs. 38.16 Stems 53.69	91.85	13.1
Poa pratensis................		.23	.52	.64	.73	.88	1.20	4.20	Lvs. 16.93 Stems .00	16.93	24.8
Andropogon scoparius.........		.95	2.05	2.79	3.31	3.47	1.50	14.07	Lvs. 47.12 Stems .00	47.12	29.8
Bouteloua gracilis.............		1.14	2.99	3.70	2.65	1.07	.47	12.02	Lvs. 19.93 Stems 44.00	63.93	18.8
Panicum virgatum (2).........				7.64	5.54	1.48	.60	15.26	Lvs. 39.89 Stems 14.09	53.98	28.2
Bouteloua curtipendula.........				3.79	2.44	3.09	1.16	10.48	Lvs. 16.88 Stems 5.15	22.03	47.5

closely compacted. The volumes of the roots of the control and clipped plants were 166 and 9.2 cc. respectively, and the dry matter 41.15 and 2.22 grams (tables II and III). Thus the volume of the roots of the clipped plants was only 5.5 per cent of that of the controls and the amount of dry matter produced was only 5.3 per cent as great.

Table III. *Dry weight and volume of roots of control and clipped plants and the per cent of dry weight and volume of the clipped compared to the control plants.*

	Dry weight of roots			Volume of roots		
Species	Clipped grams	Control grams	Per cent	Clipped cc.	Control cc.	Per cent
Andropogon furcatus (1)	2.22	41.15	5.3	9.2	166.0	5.5
Andropogon furcatus (2)	1.95	50.00	3.9	10.1	214.5	4.7
Bulbilis dactyloides	3.11	11.37	27.3	17.2	47.2	36.4
Panicum virgatum (1)	1.55	58.11	2.6	9.5	268.0	3.6
Poa pratensis	.41	1.99	20.6	1.9	10.2	18.6
Andropogon scoparius	.79	9.94	7.9	5.8	46.8	12.4
Bouteloua gracilis	.41	9.75	4.2	1.9	54.0	3.5
Panicum virgatum (2)	.92	25.59	3.6	7.2	161.5	4.4
Bouteloua curtipendula	1.46	9.32	15.6	5.0	30.0	16.6

The second series of *A. furcatus* corresponded closely to the first. When harvested, there were 41 flower stalks with an average height of 60 inches. The total amount of dry matter was 153.09 grams.

The amount of growth of the clipped sod increased after each of the first three clippings and then decreased rapidly. The total dry matter obtained from all the clippings was 28.15 grams, or 18.4 per cent as much as that of the control.

The roots of the control formed a larger mat in the bottom of the container than did those of the first series. The volume of roots of the undisturbed sod was 214.5 cc., that of the clipped sod 10.1 cc. Dry weights were 50 and 1.95 grams for the unclipped and clipped plants respectively. The amount of roots produced in the second series was greater than in the first although the amount of tops was less.

Tall Panic Grass. Panicum virgatum, also transplanted on June 28, grew more slowly than that transplanted later in the season. On August 19 the flower stalks were 16 inches tall and the panicles were beginning to open. When harvested on October 8, the foliage was 18 inches high and 40 flower stalks had developed. These averaged 30 inches in height, but some were 10 inches taller. Large, well matured fruits were produced. The total amount of dry matter was 91.85 grams.

The production of foliage by the clipped plants increased for each of the first four clippings after which there was a decrease for each of the following ones (table II). This grass seemed to be affected more by the repeated clipping than did *Andropogon*. After the fifth clipping there were only a few short stems produced. The total amount of dry matter was 12 grams, or 13.1 per cent as much as that of the control.

The root system of the panic grass was composed of many coarse, glistening white roots. All of the roots of the control extended to the bottom of the container but only a few of those of the clipped grass were so deep (fig. 3).

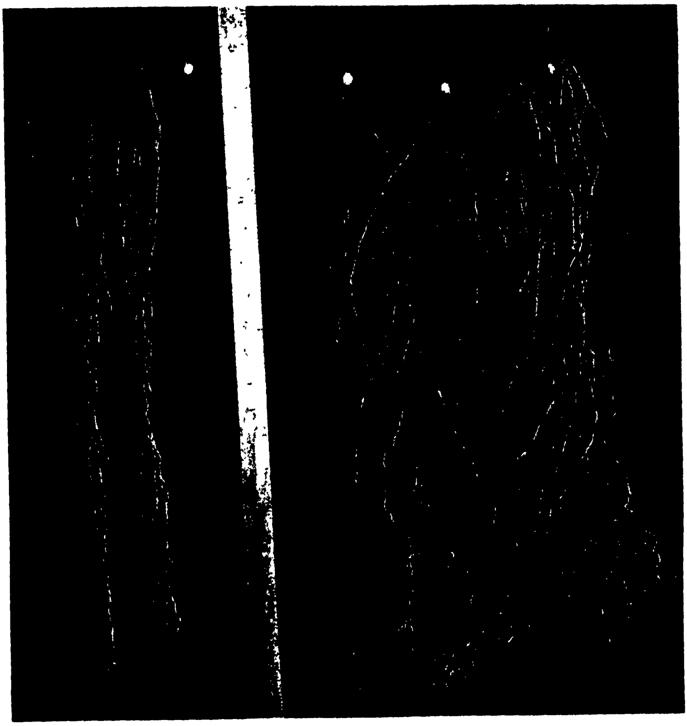

FIG. 3. Root systems of clipped (left) and unclipped *Panicum virgatum* nearly two feet long.

The differences in volume and dry matter produced by the two lots of sod were great. The volumes were 268.0 cc. and 9.5 cc., and the dry matter 58.11 grams and 1.55 grams respectively (table III).

Panicum virgatum (series 2) was transplanted on July 24. It made a very rapid growth averaging approximately 2 cm. increase in height per day for the first 12 days. This rapid development was probably due to the reserve food that had accumulated in the roots and rhizomes. At the time of harvest (October 8), 23 flower stalks were present. These averaged 23 inches in height, with a maximum of 32 inches. The total dry matter produced by the control grass was 53.98 grams. The amount of dry matter from the clipped sod was 7.64 grams for the first two-week period, while that of series 1 was only 0.57 gram. The amount of forage produced at each clipping decreased, however, after the first one (fig. 1). The grass was not clipped as many times (4 instead of 7) as the first lot and the percentage of dry matter produced by the clipped as compared to the unclipped sod was correspondingly greater, *viz.*, 28.2 as against 13.1. Neither the volume nor the dry weight of the roots was as great as that of the first lot, but the percentage between the clipped and unclipped plants was about the same. The roots of the clipped plants had only 4.4 per cent of the volume and 3.6 per cent of the dry weight of the controls (table III).

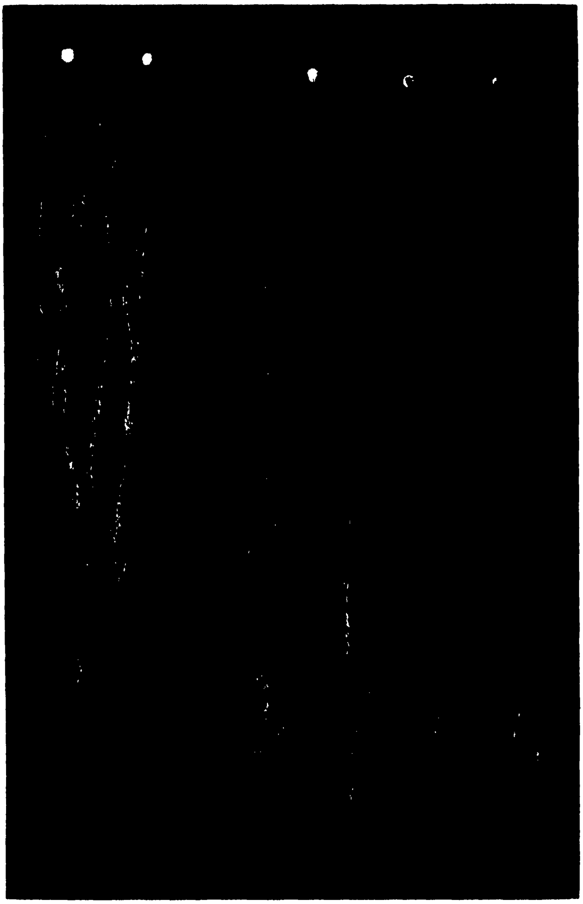

FIG. 4. Root systems of clipped (left) and unclipped *Andropogon scoparius*.

Little Bluestem. The control of *Andropogon scoparius* formed a very thick, heavy tuft of grass. A few flower stalks were developing but no fruits had been produced at the time of harvest on October 10. The dry weight of tops was 47.12 grams. The yield of tops of the treated grass increased for the first five clippings and then decreased suddenly (table II). The total dry weight of tops was 14.07 grams. An abundance of roots were produced by the control plants; they averaged 21 inches in length. Those of the clipped sod were few and had an average length of about 13 inches (fig. 4). The volume of roots was 46.8 cc. and 5.8 cc., and the dry weight 9.94 grams and 0.79 gram for the control and clipped sods respectively.

Slender Grama Grass. Bouteloua curtipendula was another species transplanted late in the season. It made a very rapid growth. When it was harvested, the 26 flower stalks averaged 21 inches in height (fig. 5). The fruits were large and well developed but were not yet mature. The total amount of dry matter of the unclipped grass was 22.03 grams (table II). The sod from which the grass was cut every two weeks did not have its growth retarded as much as did the preceding grasses. As with *Panicum virgatum* (series 2), the yield was greatest at the first clipping. At the second clipping it decreased, but again increased at the third cutting (fig. 1). The dry matter weighed 10.48 grams which was 47.5 per cent as great as that of the control.

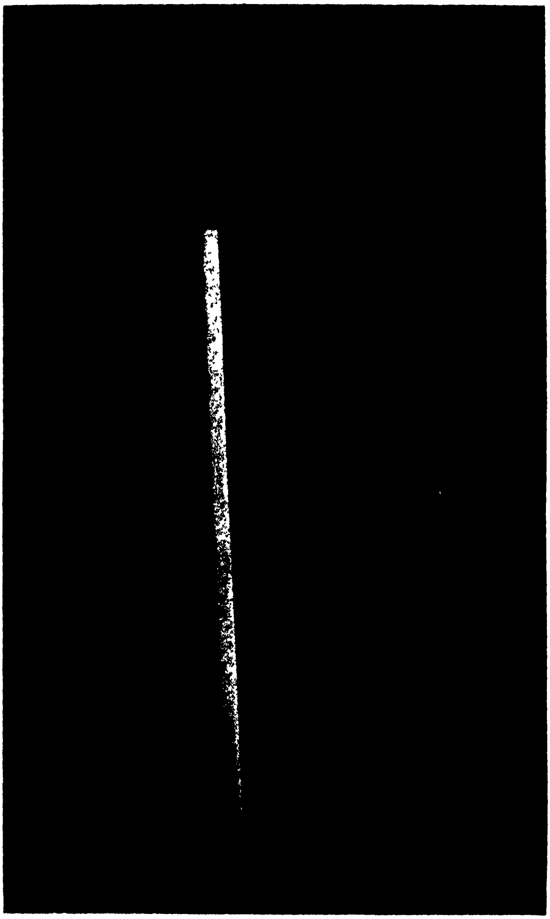

FIG. 5. Sods of *Bouteloua curtipendula* at the end of the experiment. The meter stick indicates the relative length of roots and tops. Unclipped sod at right.

The difference in amount of roots produced by the unclipped and clipped sods was not so great as for the preceding species (table III). Most of the roots of the control grass, however, extended to the bottom of the container, but only two of those of the clipped sod penetrated so deeply.

Bluegrass. Poa pratensis makes its greatest growth in the prairie during the spring and early summer. In this experiment it developed poorly throughout the hottest part of the year. The flower stalks that were produced were few and short. The total amount of dry matter of the control was 16.93 grams while that of the clipped plant was only about one-fourth as great. There was a gradual increase in amount, however, after each of the six clippings, as shown in figure 1. The percentage of dry matter produced by the clipped plants as compared to the control (24.8) was not greatly different from that of several other species. The volume of roots was 18.6 per cent and their dry weight 20.6 per cent as great as those of the control sod.

Blue Grama Grass. Bouteloua gracilis made a very fine growth which, because of a more constant water supply, was even somewhat better than that in the prairie. Very numerous flower stalks were produced which had an average height of 28 inches and yielded an abundant crop of seed (fig. 6). The total yield of tops was 63.93 grams. The amount of grass produced increased after each of the first three cuttings and then decreased after each of the three following (table II). After the clipping on August 22, flower stalks 6 inches long and flowers were produced by September 1. After another clipping on September 5, flowers were developed on stalks 3 inches long by September 12. The total amount of dry matter was 12.02 grams, which was 18.8 per cent as much as the control.

The roots of the clipped grass made a very poor growth. The average length below the sod was 9 inches, but below the unclipped sod 23 inches. The volume of the roots of the clipped plants was only 3.5 per cent as great as that of the unclipped ones, and the dry weight was 4.2 per cent as great.

Buffalo Grass. Bulbilis dactyloides differs from the other grasses in that it produces stolons. These were near the soil surface and were not removed from either the clipped or control sods until the time of the fifth clipping. There was a marked increase in dry weight of tops until the third clipping after which there was a slight but consistent decrease. The total dry matter, exclusive of the stolons, was 31.95 grams for the control and 20.17 grams for the clipped plants. The weight of stolons from the two sods differed by only 0.41 gram, those from the clipped plants (56.24 grams) being slightly lighter.

The percentage differences in volume and dry matter of roots were not so great in this grass as in the preceding since the stolons with their numerous short leaves were not removed from the clipped sod until late in the season (table III). The volume and dry weight of the clipped plants were 36.4 and 27.3 per cent respectively of the controls.

Sporobolus heterolepis and *Agropyron smithii* were not harvested. Observations were made, however, which showed that the controls had the same abundant foliage and comparatively large amount of roots as did the other control grasses, while the roots of the clipped plants were sparse.

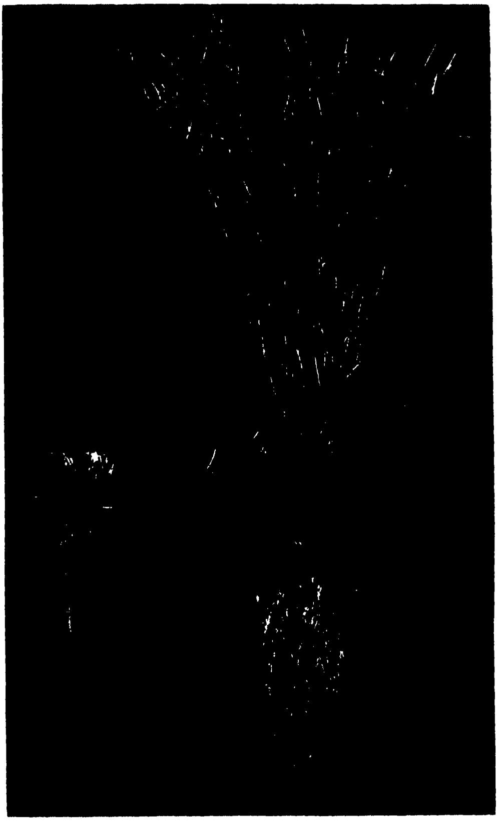

FIG. 6. Roots and tops of *Bouteloua gracilis* on October 9 which was 21 days after the fifth clipping.

EFFECT OF CLIPPING ON THE SIZE AND STRUCTURE OF ROOTS

An effect of frequent removal of the aerial parts is well shown in the relative size of the roots. The average diameter of the roots of *Panicum virgatum* was 1.5 and .96 mm. for the control and clipped sods respectively. In figure 7 the roots of the unclipped plants measured 1.6 mm., the clipped .96 mm. The width of the stele was slightly greater than that of the cortex. The average diameter of the stele was about .52 mm. for the control plants and .36 mm. for the clipped ones. The root had a pith which was surrounded by large metaxylem strands. The number of strands varied for different roots. Those from the unclipped sod ranged from 7 to 11; 8, 9, and 10 occurring most often. These averaged .062 mm. in diameter. The number of strands in roots from the clipped sod ranged from 5 to 8, 6 and 7 occurring most often. They were .05 mm. in average diameter. The number of protoxylem groups varied greatly. In the panic grass they were 4.5 to 5.5 times as numerous as the metaxylem strands. The control had 48 protoxylem points; in most cases they were composed of one strand (fig. 7). The strands averaged .021 mm. in diameter. In the treated plants there were only 32 protoxylem points, the strands of which averaged .015 mm. in diameter. The

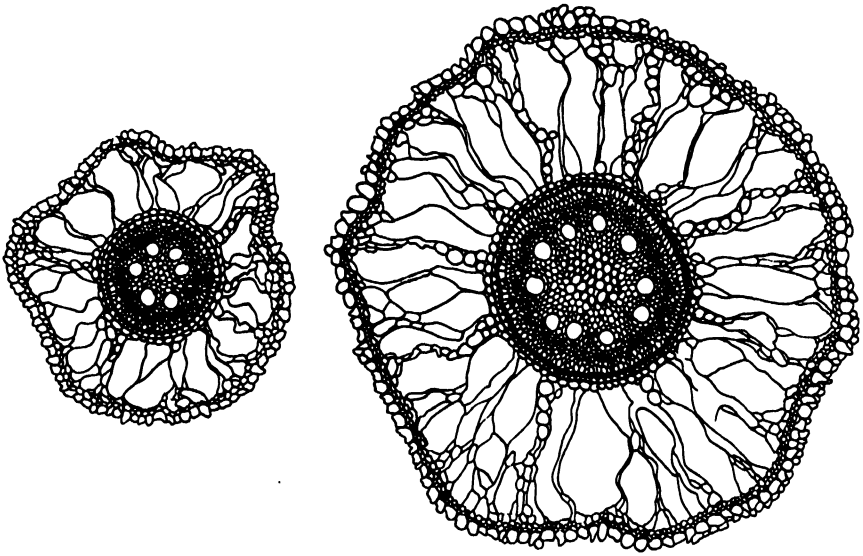

Fig. 7. Cross-sections of roots from clipped (left) and unclipped plants of *Panicum virgatum* drawn to same scale.

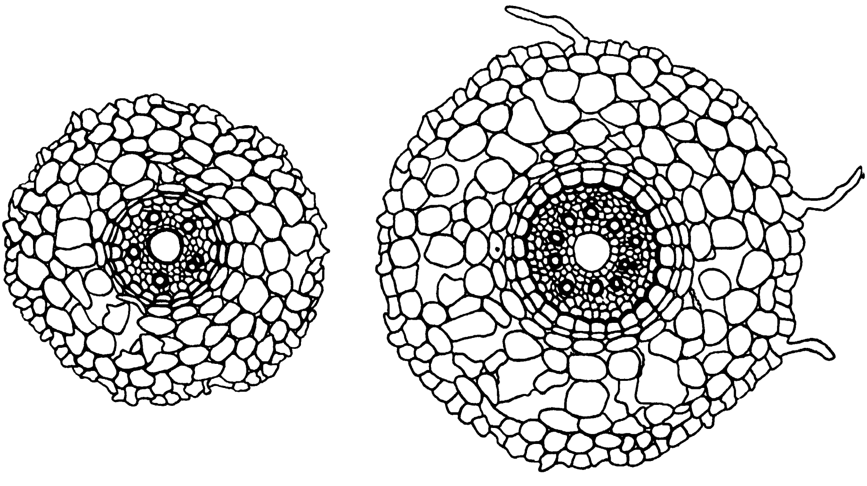

Fig. 8. Cross-sections of roots from clipped (left) and unclipped plants of *Poa pratensis* drawn to same scale.

inner tangential walls of the endodermal cells were conspicuously thickened. As the root became older the cortex began to disintegrate.

Very similar results were found for *Poa pratensis.* The differences, however, were more constant. The average diameter of the roots of the untreated grass was .38 mm., that of the treated one .29 mm. (fig. 8). Each root was characterized by a large central metaxylem vessel which had a lignified wall. The average diameter of the central vessel for the roots of the control grass was .036 mm., that of the clipped one .03. The number of protoxylem elements of the polyarch system varied from 8 to 11 for the controls, and from 4 to 6 for the roots of the clipped grass. The diameters of the protoxylem strands of the untreated and treated plants were very similar. The average diameter of the controls was .012 mm., that of the clipped plants .011 mm. The inner tangential wall of the endodermis was heavily thickened in the unclipped plants but less so where the tops had been repeatedly removed.

Resistance to Freezing

During the process of recovering the root systems from the soil in which they had grown, differences in the sods were observed. The control plants had apparently not only retained the network of living rhizomes but also had extended their area somewhat by the production of new ones. The clipped plants, on the contrary, had produced few or no new underground stems, and many of the old ones had died. Thus in the process of washing it was difficult to retain all of the original soil about the clipped plants. This accounts for the slightly smaller size of the blocks of sod, as shown in figures 2–6.

In order to determine the relation between the repeated removal of the tops and resistance to winterkilling, several of the sods were saved for further study. These included *Andropogon furcatus, A. scoparius, Panicum virgatum* (series 2), and *Bulbilis dactyloides.* They were placed in a box with moist soil packed firmly about them, covered with burlap, and transported to a dark room kept at a temperature of 5° C. A week later (October 19) duplicate sods of *Andropogon scoparius* and *Panicum virgatum* were obtained from the prairie and similarly treated. On November 2, all were placed in a refrigerator maintained at a temperature of — 12° to — 15° C. After freezing for one week they were kept at 5° C. for four days and then again frozen for a period of five days. After thawing for three days at 5° C. their temperature was gradually raised until on November 20 it reached that of the greenhouse.

Containers of the sizes already described were filled with screened loess soil of good water-content. The sods were placed in the several containers and the soil packed firmly about them. Water was added regularly as required to maintain the original weight of the container and contents. Greenhouse light was supplemented on cloudy days and between 5.30 and 8.00 P.M. each day by two 150 watt electric lights mounted in 15-inch, white, enameled reflectors suspended three feet above the tops of the containers. Care was taken that each pair of sods was equally illuminated. On December 19, *Poa pratensis* and *Stipa spartea* were obtained from the prairie, where the soil had been frozen and thawed, and added to the group. They and the preceding group of untreated plants served as controls for the species employed during the summer.

The sod of *Andropogon scoparius* that had not been clipped until the end of the summer, renewed growth 10 days after it was reset; the clipped one 10 days later. At the end of 24 days, the former had developed a thick stand of grass over 3 inches high, but the weakened sod had produced only five shoots. The control plants made a good growth and were 4.5 inches tall 5 weeks after transplanting. No further growth was made by the weakened plants, two of which were dying. Neither sod had extended roots into the new soil.

The control sod of *Bulbilis dactyloides* produced new shoots in about 10 days. At the end of five weeks a good sod 3–5 inches tall had developed but no roots extended into the soil below the sod. The grass that had been regularly clipped had been killed by freezing.

The control plants of *Andropogon furcatus* put forth many new shoots after a period of 20 days; the treated plants but two and only after 35 days. By January 31, 70 days after transplanting, the 88 stems of the control had reached a height of 15–26 inches. Growth of the clipped grass was very slow and irregular. Of the 14 stems produced, 3 were dying, and the others, which were undernourished, averaged only 4 inches in height. The control had produced a good growth of roots (4.96 g. dry weight), many of which were beginning to run along the bottom of the container at a depth of 2.5 feet. On the weakened plants there was a single root, about 2 inches long, extending below the sod.

Both sods of *Panicum virgatum,* used the previous summer, renewed growth 24 days after transplanting. At first no differences were noticeable between the two, but after a week the repeatedly clipped plants grew much more slowly. On January 18 the control grass had 64 vigorous stalks with an average height of 10 inches. The other lot had lost its deep green color, and some of the stems were dying. The 16 living shoots had a height less than one-third that of the control. These were clipped at this time. When the plants were examined two weeks later, only two stalks had made any perceptible growth, nor had any roots extended beyond the depth of the sod. The control plants, which were a foot high and thriving had developed 10 new roots, the longest being nearly 2 feet. Many new rhizomes also were starting.

Summarizing, one of the clipped sods failed to grow; two were delayed 10 to 15 days in renewing growth; and in all cases the grasses that had been repeatedly clipped produced only a very few weak shoots, some of which died. Two species had produced no roots five weeks after transplanting;

the controls of the other two had good absorbing organs but the treated plants had none.

The behavior of the sods of *Andropogon scoparius* and *Panicum virgatum* secured early in the fall and artificially frozen is of interest. They renewed growth in 14 and 25 days respectively. Both developed a fairly thick growth of shoots. After two fortnightly clippings many of the shoots failed to recover and marked deterioration of tops was evident. The dry weight of tops decreased rapidly; in *Panicum,* for example, it was 1.28, 0.78, and 0.37 g. respectively, for the several clippings. The unclipped plants had produced numerous flower stalks and a dry weight more than 4.5 times that of the several clippings. They had a great mass of roots that extended nearly 2.5 feet deep. The unclipped *Andropogon* had a good development of roots with an average depth of 13 inches; the clipped plants had produced none. *Panicum,* excavated 5 weeks after the third clipping and when the tops showed considerable recovery, had 8 roots 2 to 11 inches long.

Thus renewal of growth of these new sods was similar in time to that of the previous controls. The absence of roots in *Andropogon* was also similar. Root development, although poor on the clipped plants, was in contrast to their lack of growth on the *Panicum* weakened by clipping the preceding summer.

The two lots of *Poa pratensis* and *Stipa spartea,* both species that grow early in spring, resumed growth almost immediately, when transferred from the prairie to the greenhouse in December. Both also recovered rapidly from each of three fortnightly clippings although the yield gradually decreased. The one clipping of the control *Panicum,* for example, was 77 per cent greater than that of the several clippings. When examined after eight weeks of growth it was found that the clipped plants had developed only a few, poorly branched roots although those of the controls were quite extensive. The control and clipped plants of *Poa* weighed 0.04 and 0.64 g. respectively and those of *Panicum* 0.15 and 1.67 g. Thus the plants, although handicapped by clipping, were sufficiently vigorous to produce new roots and repeatedly regenerate the tops.

Discussion

The grasses used in these experiments are all important grazing species, *Andropogon furcatus* and *A. scoparius* alone constituting fully 70 per cent of the tall grass prairie (Weaver and Fitzpatrick, '32).

The regeneration of tops immediately after the original cutting (except for a delay in *Agropyron*) is in accord with their behavior in the prairie, two and, on low ground, sometimes three crops of prairie hay being harvested. The regeneration of tops immediately after each cutting afforded some new photosynthetic area very soon after the disturbance. Nearly all of the species commonly produce flower stalks in late autumn when mowed not later than the middle of July. Unless the herbage is removed by mowing or grazing, none save *Poa* produces much foliage after midsummer, although flower stalks may develop in abundance.

That the removal of the herbage at any time prior to the maturity of the plant was followed by more or less vigorous growth is in accord with grazing experience. Similar results were found by Parker and Sampson ('31) in their experiments with species of *Stipa* and *Bromus.*

The sods were transplanted at a time (June 28) when the growing tops had probably used considerable amounts of the root reserves, or at least before much storage for the current year had taken place. The more rapid growth of *Panicum virgatum* (series 2) and the other species transplanted later in the season (July 24) was probably due to a greater accumulation of reserve materials.

While some of the decrease in root production was to be expected, the amount of roots produced under clipping was surprisingly small. The extremely poor growth of the roots of the clipped *Bouteloua gracilis* was unexpected, since this species usually does well even under close grazing. Robertson ('32) states, however, that " In spite of clipping (of seedlings), penetration continued slowly in all species except *Bouteloua,* which responded by a gradual decrease in root length."

It seems probable that after transplanting, the production of new roots was delayed until the tops were well established. This was indicated by the delay in root growth of species transplanted in winter and verified by the experimental transplants the following summer. In one extreme case *Andropogon scoparius* produced, during a period of five weeks, an excellent growth of tops but no new roots.

Although little experimental evidence is available, it appears that the roots of grasses grow whenever the conditions are favorable and especially when the growth of shoots is not vigorous. Loeb ('24) and Janse ('25) have shown that the meristematic regions exert a profound attraction for food, water, and nutrient salts. When these regions are continually supplied with food it enables them to produce new tissues, including more meristematic tissue, which in turn further increases the demand for food. Thus there appears to exist within the block of sod competition for the accumulated food for building new roots and new shoots. These experiments indicate that for several weeks at least all or nearly all of the accumulated storage materials is used by the growing shoots and only after these are fairly well established are new roots developed. If the new shoots are again removed the process is repeated and the development of the root system is greatly retarded.

The lack of production of new rhizomes in all of the clipped sods and the death of old rootstocks, especially by winterkilling, may be directly attributed to lack of reserve food supplies and the weakened condition of the plants. McCarty ('32) has shown that in *Avena fatua* food accumulation is a factor of low or declining growth rate. " Inverse proportion has been shown to obtain between the food march and meristem activity, both vegetative and reproductive in character, and between the food march and increase in dry weight increment." Waters ('15), Aldous ('30), and other investigators have shown that cutting frequently or cutting at immaturity depletes the reserves in the roots of herbaceous plants. The bulbs of *Phleum pratense* are depleted by the rapid growth of the plants. If the plants are cut at such an interval they decrease both in vigor and yield and are more susceptible to winterkilling.

Analyses of *Agropyron smithii* showed that low yields were associated with diminished food accumulations in the subterranean organs (McCarty, '27). The lack of growth or poor growth of tops was a direct result of food depletion. Thus low capacity for survival is a concomitant of low organic food reserves. Graber ('31) found that unclipped potted plants of bluegrass produced abundant rhizomes while those that were clipped seven times produced none. Sturkie ('30) states that any cutting treatment of *Sorghum halepense* reduces the rootstock development, and the more frequently the cutting is made the greater is the reduction.

Robertson ('32) found that all but one of the six grasses with which he worked produced roots of greater diameter when the tops were uncut. Parker and Sampson ('30) showed that frequent removal of the aerial growth resulted in a poorly developed root structure, in that the diameter of the whole root, the diameter of the stele, and the number of ducts were smaller than in roots of untreated specimens of the same age.

The thinning of the cover of grass by frequent removal of the tops, as in close grazing, too frequent mowing of lawns and greens, etc., includes a similar or possibly greater decrease in the abundance of roots and other underground parts. Both of these phenomena are directly related to soil erosion. In a grass plat on a hillside in Kansas, repeated clipping had reduced the density of the vegetation to about one-third normal, including about 40 per cent weeds. A rainfall of 7.5 inches in four hours eroded away approximately two inches of surface soil, but the amounts removed from any of the other fully vegetated plats was not appreciable (Aldous, '30). Forsling ('31) states that "The increase in the density of the vegetation from 16 to 40 per cent of a complete cover and the replacement of certain plants by others with more extensive and more fibrous root systems reduced the rainfall surface run-off 64 per cent and rainfall erosion 54 per cent."

A direct relation also exists between too frequent removal of the tops, deficient root systems, and humus content of the soil. A decrease in humus results in a decreased bacterial activity since the soil population is dependent almost entirely upon the growing plant for energy material. Plants that are weakened by repeated clipping are less efficient in absorbing water and solutes. They are more subject to damage by drought, disease, and to extremes of heat or cold. They extend their area little or not at all and compete less vigorously with invaders. Invasion of weeds is an inevitable result. Not only is the annual yield of forage reduced, but the life of the plant itself is probably lessened. Moreover, the effects of reduced vigor persist for a long time. As pointed out by Robertson ('32) the greatest reduction in yield is accompanied by the greatest reduction in root development.

The common practice of pasturing tall-grass prairie a year or more before breaking so that the sod will be less dense and more easily tilled is a practical demonstration of the harmful effects upon the underground parts resulting from the close removal of tops. Harrison ('31) states that "Field observations as well as greenhouse studies show that Kentucky bluegrass cannot maintain itself under ordinary field conditions if it is cut shorter than three-quarters of an inch more frequently than once each week." The deleterious effect of frequent cutting may, however, be offset partially by cutting the plants at a greater height above the soil. Early or frequent cutting of newly seeded lawns or newly laid sod is almost certain to result in poor establishment.

SUMMARY

This paper deals with the effects of the removal of tops on root growth in soil and on regeneration and yield of aerial parts. Blocks of well established sod of seven important native pasture grasses were transplanted into large containers, grown in the field, and clipped fortnightly.

Growth of tops, which were cut upon transplanting, was resumed immediately, as well as after each subsequent cutting from July to October. The dry weight of tops of *Andropogon furcatus, A. scoparius, Panicum virgatum, Bouteloua gracilis,* and *Bulbilis dactyloides* increased for the first three to five intervals following the initial clipping, after which it decreased rapidly. The yield of *Poa pratensis* increased after each of the clippings. *Panicum virgatum* and *Bouteloua curtipendula,* transplanted in midsummer, decreased in yield after the first clipping. The unclipped grasses grew normally and in all cases, except one, produced flower stalks and seeds.

The total dry weight of tops from the clipped sods ranged from 13.1 per cent (*Panicum virgatum*) to 47.5 per cent (*Bouteloua curtipendula*) of that of the same species unclipped after transplanting. In *Bulbilis dactyloides,* where the stolons were permitted to grow, it was 63.1 per cent. In all cases there was a considerable decrease in the ground cover as the stand of the weakened grasses became thinner.

The clipped plants failed to produce new rhizomes and many of the old ones died.

The length of roots was greatly decreased, and the relative production of roots was more greatly reduced than that of tops. By volume, it ranged from 3.5 per cent of the controls (*Bouteloua gracilis*) to 18.6 per cent (*Poa pratensis*), although that of *Bulbilis dactyloides* was 36.4 per cent. The dry weight varied from 2.6 per cent in *Panicum virgatum* to 20.6 in *Poa pratensis.* The average volume of roots of the clipped sods was 11.7 per cent of that of the controls; the average dry weight was 10.1 per cent.

The roots of the clipped grasses were smaller in diameter than were those of the controls. The diameter of those of *Poa pratensis* was 76 per cent as great and those of *Panicum virgatum* only 64 per cent.

Plants weakened by repeated clipping renewed growth slowly if at all after being frozen. No new roots were produced during the period of the experiment by those that survived.

The harmful effects of the frequent removal of the cover of grasses and the accompanying deterioration of the parts underground are discussed.

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PLANT SUCCESSION ON CENTRAL TEXAS GRANITE

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The following study of plant succession was made on Enchanted Rock, a hill in the southern part of Llano County. This hill is one of several large pre-Cambrian intrusions of coarse-grained granite in the Central Mineral Region of Texas. A similar distribution of the vegetation has been found on all such intrusions visited.

According to Paige ('12), the reddish tone of the granite is largely due to potash feldspars in the form of microcline, orthoclase, and albite-oligoclase. In some of these, sodium replaces the potassium. Biotite, an iron-magnesia mica, and quartz are commonly present, while accessory minerals, such as magnetite, apatite, and titanite, usually occur.

In general the region has a rather mild climate with a mean temperature of 67.3° F., ranging from 48.7° in January to 85.2° in July. Frequent " northers " occur from November until March, often with very warm intervening periods. The average length of the growing season is 247 days, usually with no killing frosts between March 16 and November 18. The altitude, which is only 1824 feet, is not a significant factor in temperature changes.

The rainfall varies considerably, with an annual mean of 23.18 inches from 1890 to 1930. The lowest amount recorded was 9.91 inches in 1910 and the highest 49.88 in 1919. The prevailing winds of the region are from the southeast.

Bray ('01) discussed the general features of the vegetation of granitic areas and rocky slopes, but did not give a detailed analysis of the succession on granite.

TOPOGRAPHY

Enchanted Rock is a dome-shaped mass about one mile in diameter, rising 500 feet above the surrounding plain. Many depressions, cracks, and exfoliated blocks of granite mar its surface. A precipitous face on the northwest is bordered by crevices which extend from near the top to the base (fig. 1). The northeast slope is broken by exfoliation crevices four to eight feet deep and from a few inches to five feet wide. From the southeast to the west, smooth, gentle slopes afford easy approach to the top.

Several similar dome-shaped hills extend westward, while the peaks adjoining on the east are rather rugged. Passes between these occur near the 1600 foot level, and from these precipitous drainage ravines extend both to the north and south. On the southeast a flood plain of considerable depth has been formed and is covered with a forest of *Ulmus crassifolia, Quercus virginiana, Q. stellata, Q. marilandica,* and *Carya buckleyi* (fig. 2*A*). On the northwest there is a well-watered flood plain which is sheltered from the prevailing southeast winds. This plain thus supports a dense postclimax forest of *Carya buckleyi* and *Quercus stellata* whose trees are of such height and diameter as typify the true deciduous forest region. One post oak measures over three feet in diameter, and there are many trees with tall straight trunks fifty to sixty feet high.

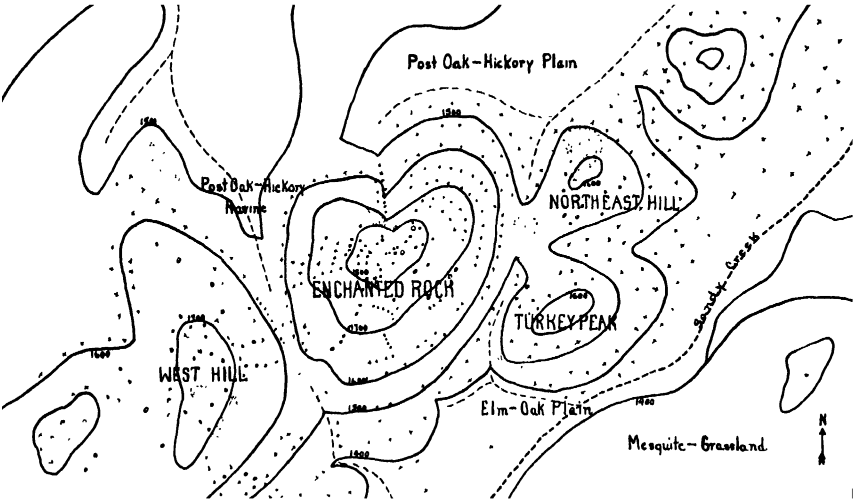

FIG. 1. Contour map of Enchanted Rock and vicinity. The principal pools are indicated by circles, gravel slopes by dots, and crevices by crosses. Contour interval 100 feet.

Sandy Creek follows the base line on the south and east, separating the granitic area from the adjoining region of schists and gneisses which is characterized by a mesquite-grassland vegetation.

SERAL VEGETATION ON THE GRANITE

Disintegration of the granite and soil deposition resulting in the formation of a habitat suitable for the climax vegetation of the region is correlated with four types of succession; namely, the rock surface, the crevice, the gravel, and the rock pool successions.

Cooper ('13) states that the conditions on Isle Royale are very severe on account of the action of waves, rain, and wind. At Enchanted Rock, conditions are still more severe, due not only to the deleterious action of the wind and rain, but also to intense heat, a high rate of evaporation, and often long periods of drought.

Modifying circumstances have, however, hastened or impeded seral prog-

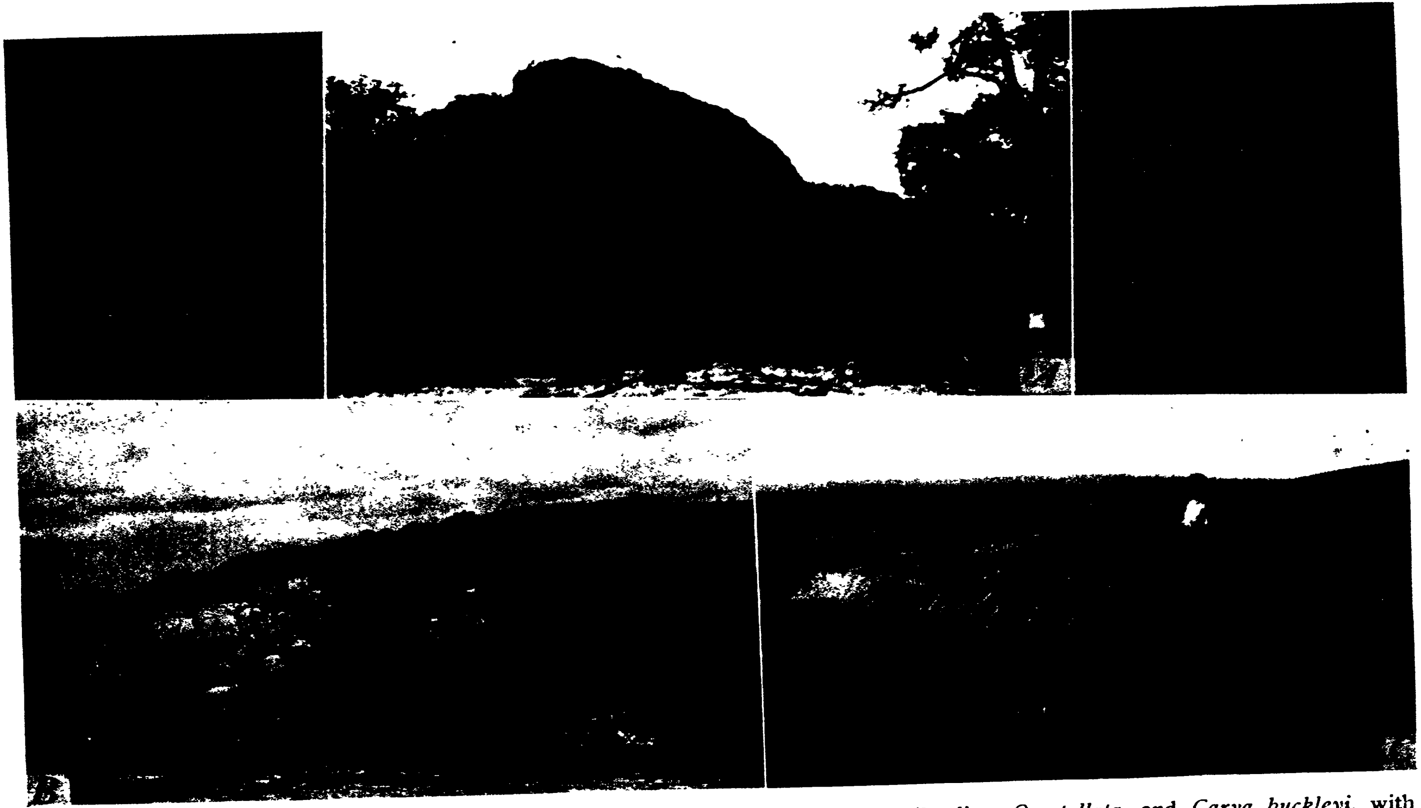

FIG. 2. *A*, Flood plain forest of *Ulmus crassifolia*, *Quercus virginiana*, *Q. marilandica*, *Q. stellata*, and *Carya buckleyi*, with *Ulmus* in the foreground, southeast of Enchanted Rock. Turkey Peak is in the background; *B*, Southwest slope showing distribution of *Verrucaria* on surface at right and *Parmelia conspersa* on the boulders at the left; *C*, Soil pocket on west hill showing several bunches of *Andropogon scoparius* surrounded by *Aristida*.

ress in some places, and have permitted the growth of mesophytes and hydrophytes in xeric surroundings. The presence of *Arisaema dracontium* in a crevice on top of one of the hills and of *Hypericum mutilum* and *Utricularia cornuta* in ravines are noteworthy.

The stages of succession along the three lines of advance in the xerosere are very similar and often comprised of the same dominants. The attainment of the climax seems to be correlated with the depth of the soil, as indicated by the presence of grassland in regions of shallow soil within a post oak-hickory forest.

The Rock Surface Succession

This succession shows the least change from season to season and from year to year. It progresses from crustose and foliose lichens, mosses, club mosses, annuals, and perennials, to grassland. Only the first four of these are well-defined, little evidence being available for the latter stages.

The Crustose Lichens. Crustose lichens occupy the greater part of the surface of Enchanted Rock. Their corrosive action is largely nullified by the immediate transport of all loosened particles through wind and water action, so that this stage is greatly prolonged. Furthermore, just as foliose forms are becoming established, exfoliation of the granite by weathering frequently exposes a new surface.

According to Fry ('27), crustose lichens have a twofold part to play in granite decomposition, causing not only chemical solution but also a certain amount of mechanical disintegration by the pull of the swelling, gelatinous apothecial or thallial tissues attached to the substratum. The composition of the granite is therefore an important factor in the distribution and ecesis of lichens. Along numerous orthoclase dikes on Enchanted Rock many foliose lichens have become established; and an outcrop of biotite is often indicated by the presence of foliose lichens in a crustose lichen zone.

Their distribution is widespread on all slopes, but they are dominant from the southeast to southwest. No lichens have been observed on surfaces so smooth as to appear polished. The invasion of foliose forms is hastened by a deposition of soil and humus such as occurs along the upper edges of small pieces of granite scattered over the entire surface. Excreta from birds also form invasion points.

The dominant crustose lichen, occupying over 90 per cent of the area, is a species of *Verrucaria* (fig. 2*B*). Its thallus is very rudimentary. In fact, after several days' rain, it does not become gelatinous enough to make footing on the rocks uncertain.

Other species present are sometimes sufficiently abundant to form a colorful display. *Acarospora chlorophana*,[1] a bright yellow-green form, is a common invader on south slopes, and *Acarospora xanthophana dealbata*, a gray-green species, is more abundant on the east. Others of a reddish-brown color,

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[1] The writer wishes to express acknowledgment to Dr. Chas. C. Plitt for the identification of the lichens.

not so widely distributed, are *Xanthorea lychnea, Acarospora synopica* (?), *Caloplaca* sp., and *Lecidia* sp. The ashy-white forms include *Lecanora cinerea* and *Haematomma punicium.* Several ashy-gray species are quite common—*e.g., Buellia spuria, Lecidia* sp., and *Lecanora frustulosa.*

The Foliose Lichens. Wherever crustose lichens have built up sufficient soil to hold enough moisture, foliose forms invade. These occur in favorable places on all slopes, but are dominant only from the northwest to northeast slopes and on boulders and trees at the base of the hill. Vertical faces of rocks, gentle slopes, and depressions may be covered.

Parmelia conspersa and *Parmelia* sp., both sea-green in color, are dominant and are chiefly responsible for the marked coloration of the area. *Physcia* sp. is associated with *Parmelia* on large exfoliated blocks of granite. Along drainage lines on all slopes *Collema flaccidum,* a black lichen with a very gelatinous thallus, is quite abundant. In a similar habitat, *Dermatocarpon* sp. is less common. *Usnea hirta* and *U. florida,* fruticose forms, frequently occur on vertical faces of blocks on the north.

The Moss Stage. The moss stage in this region is not the typical community which would be expected in a colder climate. The extreme heat, low humidity, and scanty rainfall prevent luxuriant growth and extremes of these at the reproductive period may result in the absence of capsule formation, thus indicating propagation primarily from vegetative parts. Mosses occur sparingly on old boulders, terraced granite, and newly eroded banks of ravines in regions of partial shade.

Grimmia campestris is the dominant and practically the only moss taking part in the rock surface succession. This grows in dense velvety mats and has a hoary appearance. It has been found on the south slope on large boulders and near the margin of pools and cracks on top.

The Club Moss-Fern Stage. Evidence that *Selaginella* follows the mosses has been found in a few mats. *Selaginella wrightii,* a decumbent, creeping species, precedes the invasion of *S. riddellii,* a low, erect plant. The two ferns found in moss mats are *Pellaea wrightiana* and *Cheilanthes lindheimeri.*

The Annual Stage. A few mats have been observed with annuals present. *Lechea tenuifolia, Lepidium medium, Spermolepis patens, Festuca octoflora,* and *Plantago wrightiana* may be noted. These small linear-leaved plants mature in the early spring when the temperature and moisture are most favorable. A rosette-forming annual which flowers in the autumn, *Isopappus divaricatus,* is common.

The Climax. Mats exhibiting the climax are rare, as they are easily displaced by cattle, deer, and other animals. The largest one observed was about three by six feet, one third of which was occupied by *Andropogon scoparius. Eriogonum tenellum,* a matted woolly perennial, was present, but could not be considered a dominant.

CREVICE SUCCESSION

The greater part of the vegetation found on Enchanted Rock, exclusive of lichens, is found in cracks of varying size and more or less filled with soil. Some of these must have been formed a long time ago or else they have been so favorably situated that rapid accumulation of soil has hastened the climax. In the main, succession is the same as on the rock surface, terminating, however, in a forest climax on account of the greater soil depth and larger quantities of available water.

The Lichen Stage. The lichens play little part in crevice vegetation. It is doubtful if the few observed were primary invaders of soil, since they were found on soil several inches deep. Among these are *Cladonia pyxidata, Candellariella cerinella, Diploschistes scruposus, Acarospora* sp., and *Lecidia icterica.*

The Moss Stage. The occurrence of mosses is too restricted for them to play an important part in crevice succession. *Weissia viridula* and *Fissidens incurvus,* two very similar mosses with twisted leaves, are found in crevices, as well as on gravel and on the soil in pools.

The Club Moss-Fern Stage. The club mosses are widely distributed, being found in narrow shallow cracks all over the hill. *Selaginella wrightii* is more restricted to moister cracks near the base and is not as plentiful as *S. riddellii.* The latter is probably the most important plant aiding in successional changes on the granite. Both species seem influential in soil-binding. A pH of 5.2–5.7 is found in the soil about their roots.

Based on observations on Enchanted Rock, ferns would not be included as seral dominants, but their abundance on other hills warrants their inclusion. The most important are *Cheilanthes lindheimeri* (fig. 3*D*) and *Woodsia obtusa.* The former is a hardy plant, protected by a dense scaly tomentum, while the latter is a shade-dwelling species of moist ravines and crevices.

Associated ferns are *Notholaena sinuata, Pellaea flexuosa, P. wrightiana,* and *Cheilanthes tomentosa.* The latter is not common, being restricted to shady cracks and banks. *Notholaena* has been found only over an extensive area on the southern slope of the west hill. Its range, together with that of *Cheilanthes lindheimeri,* is chiefly westward. *Pellaea flexuosa* and *P. wrightiana* seem fairly well distributed over the lower slopes and canyons, but are not abundant. Many of these ferns undoubtedly have been carried away by visitors to the Rock, but *Notholaena* grows on such inaccessible slopes that it is seldom molested.

The Annual Stage. Crevices in which the annual stage is well developed are common on top, on the upper northeast and the lower south slopes. Such cracks are usually very narrow and shallow and occur on the gentler slopes. *Sedum nuttallianum* is one of the first invaders and may often precede the fern. Many places show *Selaginella* and *Sedum* about equally intermingled; but as *Selaginella* dies out, other annuals appear which overshade *Sedum.*

The more dominant and widely distributed species are *Sarothra gen-*

tianoides, Isopappus divaricatus, Lechea tenuifolia, Galium texanum, Lepidium medium, Spermolepis patens, Croton monanthogynus, Linum multicaule, Plantago wrightiana, and *Adopogon occidentalis.* Among the grasses are *Agrostis hiemalis, A. elliottiana, Festuca octoflora,* and *Tripogon spicatus.* A

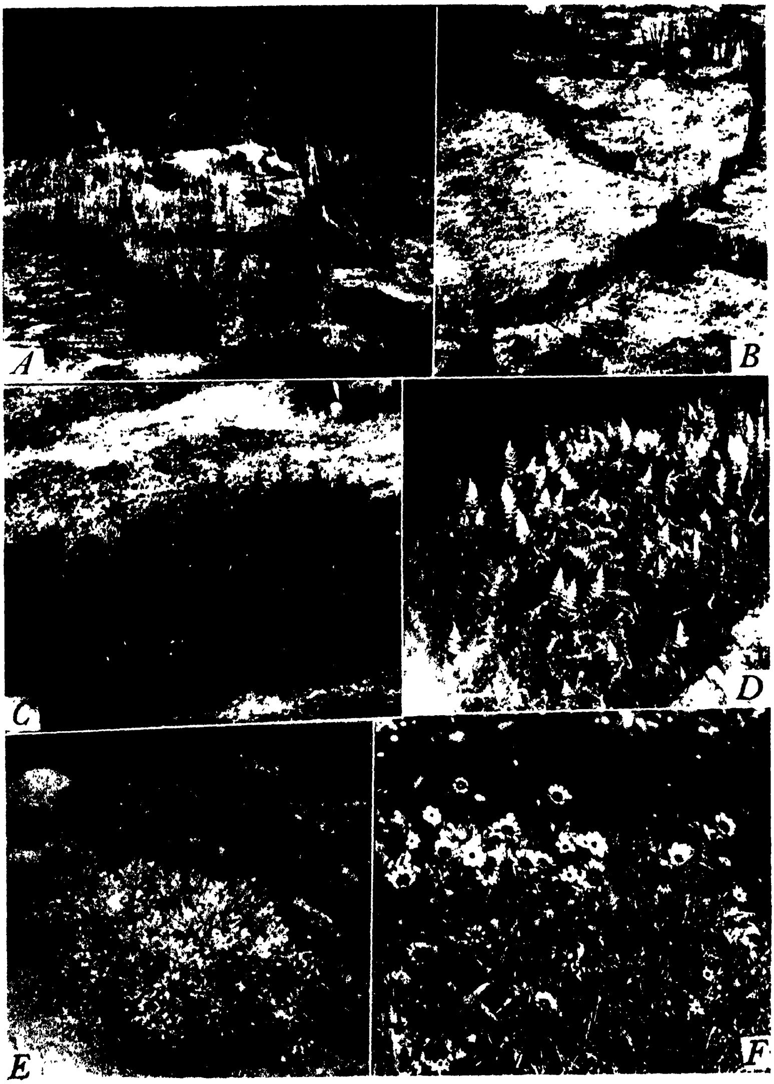


FIG. 3. *A,* Narrow cracks near the top of Enchanted Rock with *Andropogon* in the foreground. Note the dense growth of live oak in the background; *B,* Similar cracks with *Sarothra gentianoides; C, Eupatorium ageratoides; D, Cheilanthes lindheimeri; E, Eriogonum tenellum* on gravel; *F, Gaillardia pulchella* on gravel.

sedge, *Fimbristylis autumnalis,* is quite common. These are mostly low, linear-leaved plants maturing in the early spring. Many cracks are occupied almost exclusively by one species, *e.g.,* associes of *Sarothra gentianoides* (fig. 3*B*) near the top on the west and *Isopappus divaricatus* on the south.

Other species, especially abundant on the lower slopes, are *Campanula reverchonii, Paronychia lindheimeri, Polypremum procumbens,* and *Coreopsis basalis* var. *wrightii.* The vines, *Cyclanthera dissecta, Cuscuta exaltata,* and *Strophostyles helvola,* are common.

The Perennial Herb Stage. Annuals are followed successionally by perennials. Providing a colorful display in the spring and autumn, the perennials may be found in cracks a foot or more deep and often less than half an inch wide. Many such are located around the 1,600 foot level on nearly all slopes. On the west they are found near the top.

Where plenty of moisture is available, *Tradescantia gigantea, Scutellaria cordifolia bracteata,* and *Eupatorium ageratoides* (fig. 3*C*), together with the grasses, *Melica nitens, Trachypogon secundus, Panicum virgatum,* and *Triodia* sp., often form conspicuous associes. In drier crevices, *Allionia floribunda, Hedeoma serpyllifolia, Meriolix spinulosa,* and *Mentzelia oligosperma* are common. These are followed shortly by *Andropogon scoparius, A. saccharoides, Eragrostis curtipedicellata, E. lugens, Aristida purpurea,* and *A. intermedia* (fig. 3*A*).

Among the numerous vines, *Vitis candicans* and *V. cordifolia* are common in crevices on the lower slopes. There also may be found *Ipomoea lindheimeri, I. trifida, Passiflora lutea,* and *Viorna reticulata.* The latter two, together with *Ampelopsis* sp. and *Vincetoxicum reticulatum,* occur on the upper slopes.

The Shrub Stage. Xeric shrubs, such as *Yucca elata, Opuntia lindheimeri, Nolina texana, Echinocereus caespitosus, E. triglochidiatus,* and *Brayodendron texanum* replace the grasses. The smaller cacti were formerly quite abundant, but many have been carried away by visitors.

The Climax Forest. The shrubs in turn give way to scrub live oak, blackjack oak, and hickory. Hickory, *Carya buckleyi,* is uncommon on all upper slopes except the west and along the ravine on the north, but occurs frequently among the boulders on the lower slopes. Blackjack oaks, *Quercus marilandica,* are scattered on the upper slopes from the west to the northeast. Live oak, *Q. virginiana,* is widespread. Many shallow crevices are filled with shrubs two to five feet high. Deeper crevices exhibit dense stands of larger trees (fig. 3*A*). Their spreading roots are an important factor in the exfoliation of the granite.

As previously stated, these changes in succession do not always follow in clear-cut stages, nor will all consocies be present in all crevices. The distribution of the seed is an important factor in determining crevice inhabitants. Seral changes are primarily dependent upon the depth and width of the crevices, the soil, and available water.

GRAVEL SUCCESSION

On terraced slopes, particularly on the south and east and near the top on the north, are gravel deposits, resulting from erosion on higher slopes. Occasionally a deposit is due to the crumbling of lodged rocks and boulders. In a few places, particularly on the west slope of the hill to the north (fig. 1*A*) are extensive gravel beds apparently formed *in situ* from the disintegration of the granite.

Succession on the gravel takes place very rapidly, sometimes showing a marked zonation in the vegetation correlated with the depth of the soil. It follows much the same course as crevice succession, but differs particularly in the shrub components, several of which are restricted to the gravel. Among these are *Rhus virens*, *R. trilobata*, and *Styrax platanifolia*.

The Club Moss Stage. *Selaginella riddellii* is usually the initiator of the gravel succession. Its soil-binding capacity makes it particularly useful on slopes where it is found along the strategic base line of gravel deposits. Between the hills, on the blackjack-hickory slopes which are subject to much erosion, *Selaginella* is the principal floor cover.

The Sedum Stage. *Sedum nuttallianum* is accorded a stage in succession on account of its widespread distribution and zonation. In some localities it often occurs as a primary invader of gravel. Its occurrence is favored by a high content of gravel, a small amount of humus, a low concentration of H-ions (pH 5.6–6.3), and little shade.

The Annual Stage. A variety of plants may be found among the annuals invading gravel slopes, but the showiest are *Campanula reverchonii*, *Coreopsis basalis* var. *wrightii*, *Lepidium medium*, *Nama hispida*, and *Gaillardia pulchella* (fig. 3*F*). *Festuca octoflora* is the most abundant of the annual grasses.

The Perennial Herb Stage. The annuals are succeeded by hardy xeric perennials, such as *Eriogonum tenellum* (fig. 3*E*), *Achillea millefolium*, *Coleosanthus cylindraceus*, *Hedeoma serpyllifolia*, *Hymenopappus corymbosus* and the grasses, *Chloris cucullata*, *Bouteloua curtipendula*, *B. hirsuta*, *Aristida purpurea*, *Andropogon saccharoides*, and *A. scoparius*. The *Andropogons* and *Boutelouas* are dominant.

The Shrub Stage. Some shrubby plants begin to invade the grassland rather early and remain scattered among the climax trees. These are *Opuntia lindheimeri*, *O. leptocaulis*, *Styrax platanifolia*, *Brayodendron texanum*, *Rhus trilobata*, and *Yucca elata*. In some places they form an almost impenetrable stand.

The Climax Forest. The blackjack-live oak-hickory association is characteristic of the gravel succession. The trees are sometimes scattered throughout the seral vegetation, but in many places form a fairly dense, but scrubby, forest cover. The dominant trees are *Carya buckleyi*, *Quercus marilandica*, and *Q. virginiana*, but *Celtis reticulata* and *Ulmus crassifolia* occur.

The absence of post oak, *Quercus stellata,* on the slopes of Enchanted Rock and adjacent hills is noteworthy, since it is the dominant tree on plains formed from the granitic wash. The absence of live oak on the plains, as well as the presence of post oak, seems to be correlated with the depth of the water table.

The Hydrosere on the Granite

There are over a hundred small depressions or wet weather pools on the top and upper slopes of Enchanted Rock. They vary in size from one to fifty feet in length. The depth is also very variable. One of the more mature pools shows a soil depth of 27 inches in the center with a gradual decrease toward the edges. Water may be found standing in them for several days after rains. Succession takes place quite rapidly. Zonation is especially marked in oval or circular pools where soil deposition begins in the center and proceeds to the margins, causing the accumulated central mass to assume the appearance of a growing island.

There are a number of pools along lines of drainage totally lacking in soil or vegetation. The runoff is probably too swift to allow soil deposition. Many of the pools of this type on the southwest are smaller and deeper and show the accumulation of sufficient soil in the lower end to permit the attainment of grassland, but no soil deposition in the upper end.

The Submerged Stage. In pools with standing water, at least during the winter and spring, free-floating algae are abundant, forming noticeably green masses during January. A marked decay of these may be noted the latter part of February and by April little trace of them can be seen. *Spirogyra* seems to be dominant, but *Zygnema* and *Gonatonema* are abundant. *Oedogonium, Desmids,* and some of the blue-green algae have also been noted.

As soon as sufficient humus and soil are formed, the mud-rooted *Isoetes lithophila* makes its appearance. It is very abundant in many pools and has also been found in some of the streams at the base.

The Mud Plants. As the soil in a pool increases and the depth of the water becomes correspondingly less, *Tillaeastrum drummondii,* a low succulent annual, and *Riccia nigrella,* a perennial liverwort, begin to invade. They are uninjured by submergence, but thrive better on saturated soil. *Tillaeastrum* flourishes from January to April.

Associated with these, but seldom occurring in great abundance, are *Veronica peregrina, Callitriche peploides, Elatine brachysperma,* and *Leptochloa fascicularis.* All are winter or early spring plants. *Elatine* and *Callitriche* show definite consocies in many pools, but the others are scattered.

Some mention should be made here of a number of pools which display a combination of rock surface and rock pool successions. These shallow pools are formed along lines of drainage with foliose lichens aiding in soil accumulation. Some apparently do not retain enough water for algal growth, but permit distinct zones of *Tillaeastrum* and *Riccia.*

Other pools show a combination of rock surface and gravel successions. A disintegration of the granite occurs around the lower edge of these and there *Sedum* may be found, or a mingling of *Sedum* and *Selaginella,* or the latter alone. In others *Riccia* and *Sedum* occur together.

The Sedge Meadow. Low sedges three or four inches high follow *Riccia* and *Tillaeastrum* when the soil has become sufficiently deep. Dominants are *Scirpus hallii, Stenophyllus* sp., and *Cyperus inflexus.* Secondary invaders include *Juncus dichotomus* and *Fimbristylis autumnalis.* Perennial bulbous herbs, such as *Nothoscordum bivalve, Allium* sp., and *Cooperia pedunculata* are scattered. *Ibidium* sp. was noted in the autumn. A consocies of *Eleocharis capitata* constituted the only vegetation in one small pool.

The Annual Stage. The most conspicuous annuals which appear when the soil is usually more than seven inches deep are *Coreopsis basalis* var. *wrightii, Helenium badium, Lechea tenuifolia, Sarothra gentianoides, S. drummondii,* and *Sabbatia campestris.* The grasses, *Tripogon spicatus, Festuca octoflora,* and *Agrostis elliottiana* form conspicuous consocies in many pools. Low spring annuals include *Houstonia patens, H. minima,* and *Adopogon occidentalis.*

The Climax Grassland. Aristida purpurea and *Panicum lindheimeri* are among the first of the perennial grasses and so dominate the vegetation that they form marked zonations. Following these are the taller grasses, *Manisuris cylindricus* and *Eragrostis lugens.* These finally give way before the climax grass, *Andropogon scoparius,* which grows in dense tufts and stands nearly waist-high (fig. 2*C*).

While the climax has been denoted as a grassland community, some live oak, *Yucca,* and *Opuntia lindheimeri* are occasionally associated with the grasses. Their presence seems to be correlated with the occurrence of cracks in the granite.

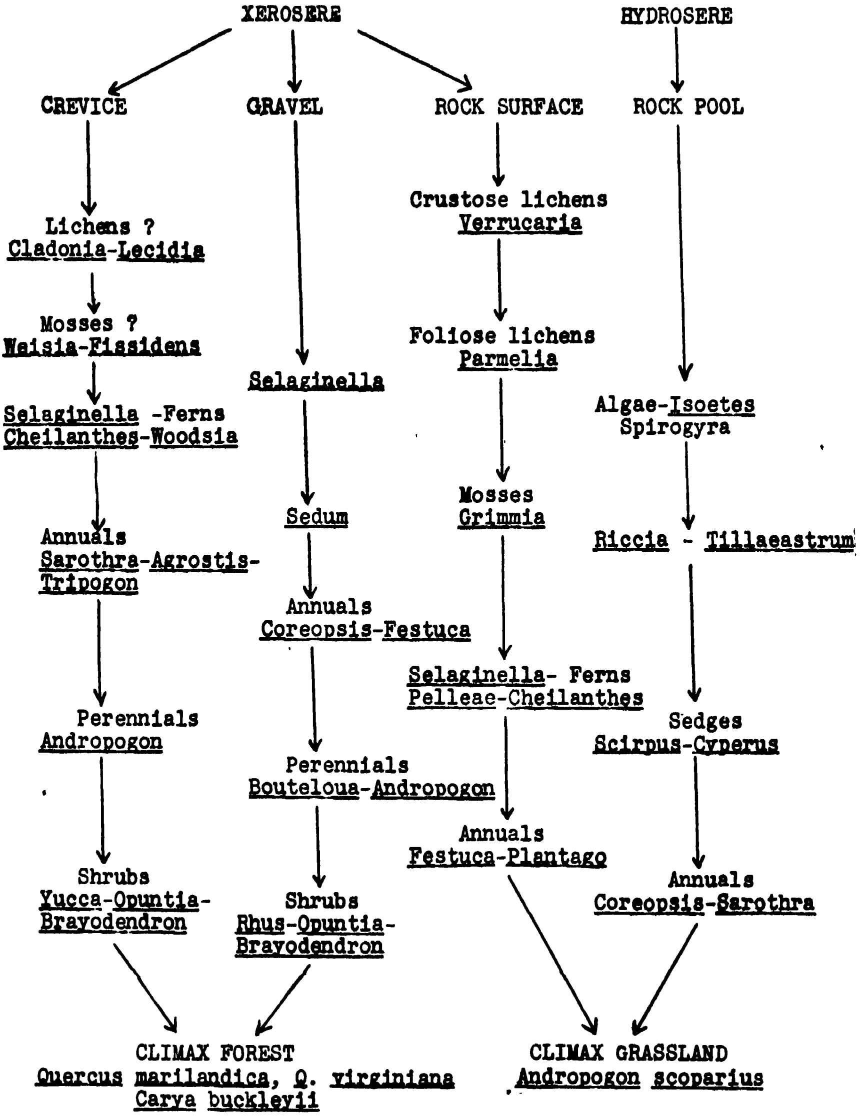
SUMMARY

The climax vegetation of the coarse granite rocks of the central mineral region of Texas is attained through four types of succession; namely, the rock surface, the crevice, the gravel, and the rock pool. The first three belong to the xerosere and the last to the hydrosere.

The vegetation of the granitic wash plains, not discussed in this paper, differs from that of the slopes in that post oak, *Quercus stellata,* replaces the live oak, *Q. virginiana.*

Successional changes on the granite are shown in table I.

TABLE I. *Successional stages on granite in central Texas.*



The Plants of Granitic Slopes

ALGAE

Gonatonema sp.
Nostoc sp.
Oedogonium sp.
Spirogyra sp.
Zygnema sp.

LICHENS

Acarospora chlorophana (Wlbg.) Mass.
" *synopica* (?)
" *xanthophana dealbata* Tuck.
Buellia spuria (Schaer.) Arn.
Caloplaca sp.
Candellariella cerinella Flk.
Cladonia pyxidata (L.) Hoffm.
Collema flaccidum
Dermatocarpon sp.
Diploschistes scruposus L.
Haematomma puniceum (Ach.) Wainio
Lecanora cinera (L.) Somerf.
" *frustulosa* (Dich.) Mass.
Lecidia icterica Mont.
" sp.
Parmelia conspersa (Ehrh.) Ach.
" sp.
Physcia sp.
Usnea hirta Fr.
" *florida* (L.) Hoffm.
Verrucaria sp.
Xanthorea lychnea (Nyl.)

LIVERWORTS

Anthoceros laevis L.
" *punctatus* L.
Asterella echinella (Gottsche) Underw.
Marchantia domineugensis Lehm. & Underw.
Oxymitra androgyna Howe
Riccia arvensis Aust.
" *campbelliana* Howe
" *mcallisteri* Howe
" *nigrella* DC.
" *trichocarpa* Howe

MOSSES

Acaulon rufescens Jaeg.
Atrichum sp.
Bartramia pomiformis (L.) Hedw.
Fissidens incurvus Schwaeg.
Funaria flavicans Mx.
Grimmia campestris Burche
Mnium cuspidatum (L.) Leyss.
Physcomitrium turbinatum (Mx.) Brid.
Weisia viridula (L.) Hedw.

PTERIDOPHYTES

Cheilanthes lindheimeri Hook.
" *tomentosa* Link.
Isoetes lithophila Pfeiffer
Notholaena sinuata (Sw.) Kaulf.
Pellaea flexuosa (Kaulf.) Link.
Pellaea wrightiana Hook.
Selaginella riddellii Van Eselt.
" *wrightii* Hieron.
Woodsia obtusa (Spreng.) Torr.

SPERMATOPHYTES

Acalypha gracilens Gray
Achillea millefolium L.
Adelia pubescens (Nutt.) Ktze.
Adopogon occidentalis (Nutt.) Kuntze
Agrostis elliottiana Schult.
" *hiemalis* (Walt.) B.S.P.
Aesculus arguta Buckl.
Allionia floribunda (Chois.) Rydb.
Allium sp.
Ampelopsis sp.
Andropogon saccharoides Swartz.
" *scoparius* Mx.
Anemone decapetala Ard.
Aphanostephus skirrobasis (DC.) Trelease
Arisaema dracontium L.
Aristida intermedia Scribn. & Ball
" *longiseta rariflora* Hitch.
" *purpurea* Nutt.
Bellis integrifolia Michx.
Bouteloua curtipendula (Mx.) Torr.
" *hirsuta* Lag.
Bradburya virginiana (L.) Kuntze
Brayodendron texanum (Scheele) Small
Bromus unioloides (Willd.) H.B.K.
Bumelia lanuginosa (Mx.) Pers.
Callitriche peploides Nutt.
Calymmandra candida T. & G.
Campanula reverchonii A. Gray
Carduus austrinus Small
Carya buckleyi Durand

Cassia lindheimeriana Scheele
Cebatha carolina (L.) Britton
Celtis reticulata Torr.
Cenchrus pauciflorus Benth.
Centunculus minimus L.
Chaetopappa asteroides (Nutt.) DC.
Chamaesyce spp.
Chloris cucullata Bisch.
Coleosanthus cylindraceus (Gray & Eng.) Kuntze
Commelina angustifolia Mx.
Cooperia pedunculata Herb.
Coreopsis basalis var. *wrightii* (Gray) Blake
Croton monanthogynus Mx.
Cuscuta exaltata Eng.
" *indecora* Choisy
Cyclanthera dissecta (T. & G.) Br.
Cyperus cylindricus (Ell.) Britton
" *inflexus* Muhl.
Draba cuneifolia Nutt.
" *platycarpa* T. & G.
Elatine brachysperma A. Gray
Eleocharis capitata (L.) R. Br.
Elymus canadensis L.
Eragrostis lugens Nees.
" *pectinacea* (Mx.) Steud.
Echinocereus caespitosus Eng. & Gray
" *triglochidiatus* Eng.
Erigeron strigosus beyrichii (F. & M.) Gray
Eriogonum tenellum Nutt.
Eupatorium ageratoides L.
Evolvulus sericeus Sw.
Eysenhardtia texana Scheele
Festuca octoflora Walt.
Filago nivea Small
" *prolifera* (Nutt.) Britton
Fimbristylis autumnalis (L.) R. & S.
Froelichia gracilis Moq.
Gaillardia pulchella Foug.
Galium texanum (T. & G.) W.
Gnaphalium purpureum L.
" *wrightii* A. Gray
Hedeoma serpyllifolia Small.
Helenium badium (Gray) Greene
Helianthemum rosmarinifolium Pursh.
Hordeum pusillum Nutt.
Houstonia angustifolia Mx.
" *minima* Beck.
" *patens* Ell.
Hymenopappus corymbosus T. & G.
Hypericum mutilum L.
Ibervillea lindheimeri (Gray) Greene
Ibidium sp.
Indigofera argentata Rydb.
Ipomoea lindheimeri A. Gray.
Isopappus divaricatus (Nutt.) T. & G.
Juncus dichotomus Ell.
Laciniaria punctata (Hook.) Kuntze
Lepidium medium Greene
Leptochloa fascicularis (Lam.) Greene
Lepuropetalon spathulatum (Muhl.) Ell.
Lechea tenuifolia Mx.
Leptilon canadense (L.) Britton
Leptoloma cognatum (Schult.) Chase
Lespedeza frutescens (L.) Britton
Lesquerella sp.
Limnodea arkansana (Nutt.) Dewey
Linaria texana Scheele
Linum multicaule Hook.
Lithospermum angustifolium Mx.
Lonicera alba T. & G.
Lotus americana (Nutt.) Bisch.
Manisuris cylindricus (Mx.) Ktze.
Meibomia sessifolia (Torr.) Ktze.
" *wrightii* (Gray)
Melica nitens Nutt.
Mentzelia oligosperma Nutt.
Meriolix spinulosa (T. & G.) Heller.
Metastelma barbigerum Scheele
Mollugo verticillata L.
Monarda clinopodioides Gray
Nama hispida Gray
Nazia aliena (Spreng.) Scribn.
Nolina texana (Torr.) S. Wats.
Nothoscordum bivalve (L.) Brit.
Opuntia leptocaulis P. DC.
" *lindheimeri* Eng.
Panicum perlongum Nash
" *scribnerianum* Nash
" *lindheimeri* Nash
" *virgatum* L.
Paronychia lindheimeri Eng.
Parosela carnescens Rydb.
Paspalum pubescens Muhl.
Passiflora lutea L.
Phacelia congesta Hook.
Phalaris caroliniana Walt.
Phlox drummondii villosissima Gray
Phyllanthus polygonoides Nutt.
Phytolacca decandra L.
Plantago virginica L.
" *wrightiana* Decne.

Polypremum procumbens L.
Polypteris callosa (Nutt.) Gray
Portulaca pilosa L.
" *lanceolata* Eng.
Quercus marilandica Muench.
" *stellata* Wang.
" *virginiana* Mill.
Ranunculus macranthus Scheele
" *tener* Mohr.
Rhus copallina lanceolata Gray
" *toxicodendron* L.
" *trilobata* Nutt.
" *virens* Lindh.
Rudbeckia hirta L.
Sabbatia campestris Nutt.
Sagina decumbens L.
Sarothra gentianoides L.
Scirpus hallii Gray
Scutellaria cordifolia bracteata (Benth.) Small
Sedum nuttallianum Raf.
Senecio ampullaceus Hook.
" sp.
Silene antirrhina L.
Smilax bona-nox L.
Sonchus asper (L.) All.
Sophora affinis T. & G.
Specularia biflora (R. & P.) Gray
" *leptocarpa* (Nutt.) Gray
Spermolepis patens (Nutt.) Robinson
Sphenopholis obtusata (Mx.) Scribn.
Stenophyllus sp.
Stipa leucotricha Trin.
Streptanthus platycarpus Gray
Strophostyles helvola (L.) Ell.
Styrax platanifolia Eng.
Talinum parviflorum Nutt.
Thelesperma trifidum (Poir.) Britton
Tithymalus arkansanus (Eng. & Gray) Kl. & Garcke.
Trachypogon secundus (Presl.) Nash
Tradescantia gigantea Rose
" *occidentalis* Britton
Triodia pilosa (Buckl.) Hitch.
" sp.
Tripogon spicatus (Nees.) Eckman
Ulmus crassifolia Nutt.
Ungnadia speciosa Endl.
Urtica chamaedryoides Pursh.
Utricularia cornuta Michx.
Valota saccharata (Buckl.) Chase
Verbena officinalis L.
" *pumila* Rydb.
Veronica peregrina L.
Viburnum rufidulum Raf.
Vincetoxicum reticulatum (Eng.) Heller
Viorna reticulata (Walt.) Small
Xanthoxalis stricta (L.) Small
Zornia bracteata (Walt.) Gmel.

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REVIEWS

Colony-founding among Ants[1]

The book is an outcome of Dr. Wheeler's trips to Australia in 1914 and 1932. He found there an extraordinary population of the most primitive ants, the Ponerinae, which are represented in this country by rather degenerate remnants. In Australia they are dominant, large, alert, formidable ants. Something of the habits of 31 species is recounted.

The author discovered that the female, after a nuptial flight, founds a colony alone by digging a cell under a stone or log from which she forages to collect nectar for herself and soft bodied insects for her larvae. This wasp-like behavior is contrary to the habits of higher ants in which the female encloses herself in a cell and fasts, or eats some of her eggs, until her first offspring are adult. The difference seems to be due to the fact that the higher ants have substituted morphological specializations (large size, fat, wing muscles) for a behavior instinct (foraging).

From his studies of the very primitive *Myrmecia*, Dr. Wheeler draws a picture of the ancestral Proformica. The ants were terrestrial and after her flight the female built a cavity in soil from which she foraged. The eggs were scattered singly because the salivary glands were probably poorly developed and the ant could not glue them together. This may have precluded many myrmecophyles. The larvae were fed on fresh, killed insects while the adults ate nectar. The female was not much larger than the worker and was less fecund than the more highly specialized modern ants.

The contention is strongly supported that the ants were always haplometrotic, that is a single female founds the colony instead of its being founded by several to many cooperating females. Since the Formicidae are really a family of Vespoid wasps it seems logical that this colony formation is an outgrowth of progressive provisioning of the nest, in which the mother wasp stays with her larvae and feeds them from day to day. From this the next step is the mother remaining with her adult offspring, and so founding a colony. Development of the social life of various groups of wasps and bees is discussed in connection with this problem.

The author believes that parthenogenesis plays some part in the adoption of a purely feminine type of society because even in the solitary ancestral Aculeata the parthenogenetic males are specialized for fecundation only and so can take no part in the social life.

The origin and behavior of the worker class are explained as being merely

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[1] **Wheeler, William Morton.** 1933. Colony-founding among Ants. Pages viii + 179, 29 figs. *Harvard University Press.* $2.00.

modifications of the female behavior, which is essentially that of a solitary wasp. The morphological inferiority of the worker is due to alimentary castration in the larval stage and nutricial castration (from *nutrix*, a nurse) in the adult. In the highly specialized groups having dimorphic workers the deviations from the primitive type may be due to qualitative as well as quantitative differences in feeding. The worker is more alert and versatile than the female and has a more expanded world about her because her brain is less powerfully influenced by her ovaries. The nervous systems are not different in the two.

MARY TALBOT

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PROTECTIVE COLORATION [1]

There are times when observations of natural experiments indicate a more accurate control of factors than observations of rigid laboratory experiments. This is particularly true when the time factor is important. Benson has made an admirable study of the mammals, particularly the rodents, on isolated black lava beds and white sands of the Tularosa Basin in New Mexico. He notes the distribution of each form in relation to climatic, physical and biotic factors and describes the color variations and distribution of pigment. He assumes, on the basis of Sumner's work, that the color variations are hereditary. He is able to show quite conclusively that the color variations of a number of genera are correlated with the color of the background and do not show correlation with climate, humidity, temperature or food. He discusses at length the possibility of natural selection toward background color together with isolation operating as evolutionary mechanisms in the case of these rodents and concludes that these indeed are the significant environmental influences. McAtee's recent work on the significance of protective devices of the organisms eaten by birds is critically discussed.

It seems that such careful field work by individuals trained in taxonomy and general biology will do much to aid in the development of our knowledge concerning speciation mechanisms and the great rôle played by various environmental factors in influencing the precise direction of evolution.

ALFRED E. EMERSON

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PLANT ECOLOGY FOR THE LAYMAN

Scientists should realize an obligation to the general public in the matter of bringing to the layman some of the results of the investigations of the specialist. This obligation seems to be generally admitted and also very generally neglected. It is therefore pleasing to find from time to time successful attempts on the part of plant scientists both to recognize and discharge the

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[1] **Benson, Seth B.** 1933. Concealing coloration among some desert rodents of the southwestern United States. *Univ. California Publ. Zoology*, **40**: 1–70, 2 pls., 8 figs. $1.25.

obligation. A recent publication by the University of North Carolina will certainly carry the results of ecological studies into many homes in the State and will furnish a model that other universities may well follow.[1]

In this volume, which is dedicated to the members of the Garden Club of North Carolina, Wells has organized his material under the general headings of "The natural gardens of North Carolina" and "The herbaceous wild flowers of the natural gardens." The first consists of descriptions of the principal plant communities of the State, the second of descriptions of the chief individual plant species.

The ecological descriptions are in non-technical language that may at times be criticized as teleological. The personification of the trees and flowers, while objectionable to the scientist, may be pardoned when it accomplishes its object in enlisting the interest of the non-scientific reader. The scope of the discussion and something of the style may be gathered by samples from the chapter headings: "The windy dunes and marine oak forest," "Cattails and their neighbors," "Fish gardens; aquatic vegetation," "Where winter never comes; the evergreen shrub-bogs," "The most beautiful gardens; the savannas or grass-sedge bogs," "Deserts in the rain," "The melting pot; old fields where plant foreigners and natives mingle" and "Christmas tree land; the boreal forests of our high mountains."

The facts presented in this ecological discussion seem to be well selected, accurately stated and of a nature that will enable the intelligent lay reader to enjoy the landscapes of grassland, forest and mountain with a more intelligent interest. This interest will be increased by the 123 illustrations in this part of the book, which covers 208 pages.

In the second part of the book are found keys and descriptions intended to lead to the recognition of individual plant species. The seven keys are for the plants of seven great community types. They are for the herbaceous plants of great forest uplands, sandhills, coastal dunes, savannas, fresh water marshes, salt marshes, and aquatic plants. In the keys flower color and leaf form play an important part and the general scheme seems a promising one.

The descriptions of individual species are brief and simple but aided by the numerous illustrations will be found very useful.

The book is well printed, attractively bound, and well illustrated.

GEO. D. FULLER

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MOORS IN SOUTHWESTERN FINLAND[2]

This study of the plant associations and stratigraphy of a series of moors located in southwestern Finland within an area 50 kilometers wide and ex-

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[1] **Wells, B. W.** 1932. The natural gardens of North Carolina. 458 pp., 209 figs. *The University of North Carolina Press, Chapel Hill, N. C.* $3.50.

[2] **Aario, Leo.** 1932. Pflanzentopographische und Paläogeographische Mooruntersuchungen in N-Satakunta. Communicationes Instituti Forestalis Fenniae, 17(1): 1–190. 22 figs., 42 tables. Helsinki.

tending inland 150 kilometers from the coast may be divided into two parts. The first deals with the factors which bring about the formation of various types of moors together with a description of their plant cover. The second is a study of the fossil content of the peat for the purpose of determining past climatic changes.

During the past 9000 years the western coast of Finland has risen approximately 200 meters. This change in elevation has resulted in the formation of numerous moors of different ages which have afforded the author an excellent opportunity for a comparative study of their development. The common cause of moor formation in this locality is the accumulation of surface or ground water in shallow depressions in the forest or in the open. Comparative studies show that the stratigraphy for corresponding periods of time is the same in all the moors of the region.

Aario presents some interesting data regarding the correlation of present pollen spectra with the composition of present forests. He found that in a number of sections where the spruce is the dominant tree, its percentage in the pollen spectrum amounted to only 21 per cent. In contrast, the birch, pine, and alder, although not as common as the spruce, are represented by a much higher percentage. Often an increase of one type of pollen in a pollen spectrum means a decrease of another although the number of both types in a given community be approximately the same. These facts are of utmost importance in the interpretation of pollen diagrams. Climatic changes or plant invasions can be best interpreted from pollen diagrams not so much by the increase or decrease of certain genera as by the appearance or disappearance of the genera during the development of the moor.

Taking into consideration the important criticisms of pollen analysis, Aario draws the following conclusions from the pollen counts of 120 moors in southwestern Finland:

1. The last ice sheet apparently receded during the Ancylus period since the first trees to invade the newly formed land were the elm, linden, alder, birch and pine. The climate during this stage was probably dry since pine was the dominant tree and warm indicated by the presence of elm and birch.
2. Following the pine maximum there was a decided increase of birch.
3. Toward the close of the birch period which occurred about 2500 B.C., the spruce appeared and soon became the dominant tree.
4. The last stage shows a decrease of spruce and an increase of pine.

Macroscopic remains of typical southern plants such as *Najas flexilis*, *Carex pseudocyperus* and *Trapa natans* were found in the strata representing the transition between the Ancylus and Littorina periods. Aario believes that their absence during later periods is due not to climatic but to edaphic factors.

Aario's paper is well organized and adds much to our knowledge of the ecology of northern moors.

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NOTES AND COMMENT

The Effect of Humidity upon the Rate of Evaporation

A large amount of data has been taken in the past upon various phases of evaporation, but so far as we have been able to learn data have not been taken over a large range of values of relative humidity under control in the laboratory. The work up to the present has been done in the open and the variations have been such as naturally occur together with temperature variations and other variable conditions. From these data several more or less complicated formulae have been established which are supposed to give the rate of evaporation.

There are several things that affect the rate of evaporation. The more important of these are: (1) Temperature of the water and that of the surrounding air which may not be the same; (2) The relative humidity of the air over the surface of the water; (3) The pressure of the air above the surface; (4) The velocity of the air across the surface; (5) Area of the surface; and (6) The so-called rim effect.

In our present problem we have interested ourselves in only one of these—the effect of humidity of the air above the surface.

A vessel, 9¾ inches in diameter and 13½ inches deep, was placed into the water of a constant temperature bath. On the bottom of this vessel there was placed another vessel containing the saturated solution of a substance of known chemical composition for the humidity control with some of the solid phase present to insure saturation. A third vessel, a weighing bottle 3 cm. deep and 5 cm. in diameter, was filled to a certain depth with distilled water and after being weighed was placed into the solution. The reason for placing this vessel into the solution was to increase the probability that its temperature would be that of the air inside, since evaporation would cause the water to cool. A fan run by a shaft through the cover of the large vessel kept the air over the liquid in constant and uniform circulation during the time that evaporation was taking place. The vessel was allowed to stand in this condition for from 12 to 24 hours depending upon the rate of evaporation, after which the small vessel containing the water was removed and again weighed. The constant temperature bath was adjusted to hold the temperature to probably less than a tenth of a degree variation from 20° C. The data for the substances used to control the relative humidity were taken from the International Critical Tables, Vol. I, p. 67. We are informed that the values given in these tables are as accurate as relative humidity can be measured. A summary of the data is contained in table I.

The data taken show that, when all other factors are kept constant, the rate of evaporation is proportional to (100% — R.H.) where R.H. is the relative humidity of the air above the surface from which evaporation is taking place. The significance of the results is shown by the curve that follows (fig. 1). The rate of evaporation is plotted on the x-axis and (100% — R.H.) on the y-axis.

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TABLE 1. *Relation between relative humidity and rate of evaporation*

Substance	LiCl	$KC_2H_3O_2$	CrO_3	KCNS	$Na_2Cr_2O_7$	NaBr	$NaNO_2$	NH_4Cl	K_2HPO_4	$Pb(NO_3)_2$
Relative humidity	15%	20%	35%	47%	52%	58%	66%	79.2%	92%	98%
No. of trials	3	3	3	2	3	2	3	2	3	3
Average rate of evaporation in milligrams per hr.	161.1	151.3	121.6	106	89.4	80.7	66.2	41.3	19.9	7.86
Maximum per cent of variation of rate of evaporation from average value	0.3%	1%	1%	2%	2.3%	0.3%	0.3%	2%	4%	3%
Evaporation rate in milligrams per hr. per $cm.^2$	8.16	7.66	6.16	5.38	4.52	4.09	3.35	2.09	1.01	0.398
Average barometer reading	58.37 cm.	58.45	58.34	58.45	58.13	58.39	58.68	58.30	59.10	58.95
Maximum variation of barometer during trials	0.04 cm.	0.18	0.10	0.08	0.19	0.05	0.01	0.15	0.15	0.20

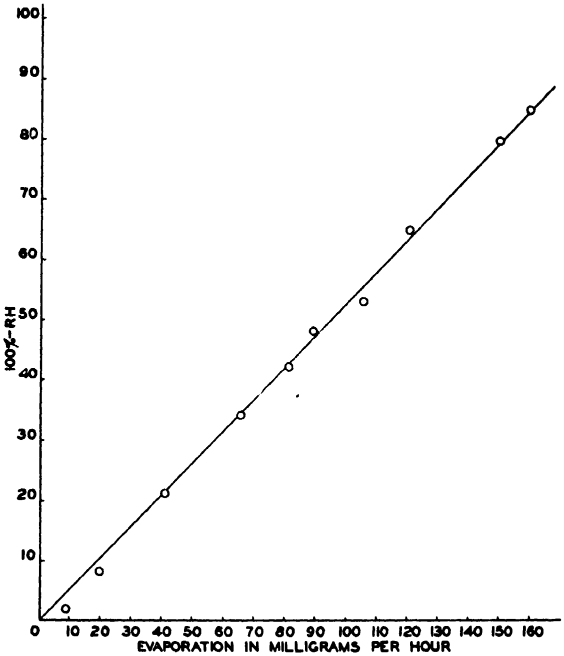

FIG. 1. Curve showing relation of rate of evaporation to relative humidity.

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INDEX TO ECOLOGY, VOLUME XIV, 1933

Date of issue.	Date of issue.	Date of issue.
17-7-40		
1-8-40		
19-11-42		
10.12.45		
4.1.51		
19.2.57		
7-6-56		
15-5-58		
29.10.59		
5.1.1961		